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Observations on the Oil and Component Fatty Acids of the Oil from Newfoundland Capelin[1]

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ABSTRACT

The oil recovery from beach-spawning Newfoundland capelin has confirmed an earlier report that the fat content is of the order of 3–4%. The oils recovered from both sexes were examined, that from the female having a significantly higher iodine value. Owing to the sex ratio on the beach a commercial oil might be essentially that from the male capelin and is similar in properties and distribution of major fatty acid components to herring oil. The content of unsaponifiable matter was somewhat higher than in commercial herring oil.

INTRODUCTION

The capelin, *Mallotus villosus* (Müller), has been at various times and in different areas of the world an important commercial fish (Pitt, 1958; Møller and Olsen, 1962), although at present there is no large processing industry in Canada dependent on this species. In addition to the more familiar seasonal shore spawning population (Templeman, 1948a) there is also a Grand Banks spawning population (Pitt, 1958). Although not as satisfactory as herring as a source of oil, the processing of any large amount of capelin for meal would inevitably yield oil as a valuable by-product. No recent local study of this oil has been reported and an examination was therefore considered desirable to establish those properties of commercial interest and as a preliminary exploration of the component fatty acids. Since it is likely that only the shore spawning population would be involved this investigation is restricted to such fish.

EXPERIMENTAL

Source, Sampling, and Oil Recovery

The fish were caught at Torbay, Newfoundland, about 9 p.m. on June 27, 1962. The method of fishing was a dip net and this was employed on a school of fish swimming near the beach in shallow water. Owing to the spawning habits the ratio of males to females thus caught was 17.3:1, although this would not apply to catches further offshore (Templeman, 1948b). The fish were iced overnight and frozen the following morning while still in rigor, being packed in dry ice for shipment to Halifax, N.S. Only unspawned females were selected for the examination of this sex.

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The frozen fish were thawed in cool water and measured individually for length from nose to tip of tail fin (Templeman, 1948c) but the weight was taken only *in toto*. The fish were macerated in a Waring Blendor and mixed with anhydrous sodium sulphate, employing about 2 kg for the female flesh (2.2 kg) and 2.7 kg for the male flesh (1.4 kg). The respective lots were stirred into approximately 5 l benzene and allowed to stand overnight, followed by suction filtration and stripping off of the benzene under vacuum. All operations were carried out in so far as possible in a nitrogen atmosphere. The pertinent sampling data and the gross properties of the oil are summarized in Table I. The saponification value, iodine value and percentage unsaponifiable matter were determined according to Official American Oil Chemists' Society Methods.

TABLE I. Data relating oil yield and properties to average size and sex of capelin.

	Females	Males
Number of fish	56	52
Maximum length (cm)	17.5	19.4
Minimum length (cm)	13.8	16.1
Average length (cm)	15.8	17.9
Total weight (g)	1407	2251
Average weight (g)	25.1	43.3
Weight oil extracted (g)	47.7	75.3
Oil as % wet fish	3.39	3.35
Iodine value (Wijs)	144.2	125.5
Refractive index (n_D25)	1.47760	1.47471
Percentage unsaponifiable matter	5.9	4.1
Saponification value (mg KOH/g)	179	183

PREPARATION OF METHYL ESTERS

Samples of fatty acids from the respective capelin oils after removal of the unsaponifiable matter were esterified with boron trifluoride–methanol reagent (Metcalfe and Schmitz, 1961). Samples of methyl esters were also prepared by standard alkali-catalysed interesterification. For examination by fatty acid chain length hydrogenations were carried out on a semi-micro basis (Vandenheuvel, 1952). Hydrogen values for the esters by the latter procedure agreed satisfactorily with the Wijs iodine values for the oils.

GAS–LIQUID CHROMATOGRAPHY OF COMPONENT FATTY ACID ESTERS

The apparatus employed was a Wilkens Aerograph[3] A-90, with a column of copper tubing 10 feet long and $\frac{1}{4}$ inch O.D. The column packing was 20% commercial ethylene glycol succinic acid polyester on 60–80 mesh GC-22 Super Support[4]. Helium was employed as the carrier gas at 20 psi input, the filament

[3]Wilkens Instrument and Research, Inc., Walnut Creek, Calif.
[4]The Coast Engineering Laboratory, Hermosa Beach, Calif.

current was 250 ma, and the injection port and oven temperatures were respectively 250° and 220°C. Identifications assigned to peaks were on the basis of comparison with other data (Ackman *et al.*, 1962). No essential difference was observed between the samples prepared from fatty acids free of unsaponifiable matter and those prepared by interesterification.

DISCUSSION

Oil

The oil yield in the present study (Table I) agrees with a previous report on beach spawning capelin indicating 3–4% fat (Andrews, 1954). Pelagic capelin may have fat contents as high as 23.4% (Møller and Olsen, 1962). This is comparable with some Atlantic herring, where, dependent on the season, the oil content may run from 4.1 to 17.4%, and the low values are also associated with the spawning period (Leim *et al.*, 1957). The procedure employed in the extraction has been found in this laboratory to be equal to common extraction techniques in efficiency and much more convenient in practice. It is, however, possible that this procedure is responsible for the amount of unsaponifiable matter being higher than in commercial herring oil which is produced under completely different conditions.

The unsaponifiable matter in the female capelin oil had a brighter yellow colour than that from the male capelin oil. This is probably derived from the eggs. Bailey (1952) mentions that oil from salmon eggs has a brighter colour than that from the flesh. Despite the high yield, the unsaponifiable matter was completely soluble in diethyl ether and petroleum ether, indicating the absence of non-lipid materials.

In an industry based on beach spawning capelin the oil would be essentially that from the males if the fish were caught in the surf, but if caught somewhat further out, which might be more practical for large-scale operations, the oil would be essentially that from unspawned females. Dependent on market specifications, etc., particularly in regard to iodine value, it might be desirable to consider processing of the catch on a sex basis if this were practical.

Fatty Acids

Despite the numerous advantages of gas-liquid chromatography in the oil analysis field, the simple application of this technique to marine oils suffers from two disadvantages: the lack of individual quantitative standards (Kaufmann *et al.*, 1962), and the overlapping by chain lengths (Ackman *et al.*, 1962). In the first instance the area percent data given in Table II for some of the major acids of capelin oils is therefore only approximately comparable with weight percent, the bias being a deficiency in the response obtained for the longer chain and/or more highly unsaturated fatty acids. In Table III the chain length distribution has been adjusted to weight percent by the application of correction factors (Horrocks *et al.*, 1961) which reduce the average deviation with known samples from 4.7% to 1.7%.

TABLE II. Gas–liquid chromatography area percent response for some major component fatty acid methyl esters from capelin oils.

Component[a]	Probable double bond positions[b]	Female	Male
14:0	–	8.6	8.8
16:0	–	13.3	12.0
16:1	9	16.5	14.9
18:0[c]	–	1.6	1.8
18:1	9	10.7	9.0
20:1	11	17.2	21.5
20:5	5, 8, 11, 14, 17	8.6	5.8
22:1	13	14.2	18.5
22:5	7, 10, 13, 16, 19	0.9	0.5
22:6	4, 7, 10, 13, 16, 19	4.8	3.6
Other	–	3.6	3.6

[a]Notation gives — chain length: number of double bonds.

[b]Structures are those suggested by Ackman *et al.*, 1962, for corresponding major components of seal oil.

[c]Error may be large owing to small peak size and probable superposition of component peaks.

TABLE III. Chain-length distribution of component fatty acids of capelin oil as indicated by gas–liquid chromatography of hydrogenated methyl esters.

	Female		Male	
Component	Area response	Weight	Area response	Weight
	%	%	%	%
C_{14}	7.7	7.2	8.3	7.6
C_{15}	0.9	0.9	0.5	0.5
C_{16}	29.7	28.4	28.5	27.3
C_{17}	0.5	0.5	0.9	0.9
C_{18}	13.1	13.0	11.0	10.9
C_{19}	0.3	0.3	0.1	0.1
C_{20}	25.6	26.3	28.3	29.1
C_{21}	0.2	0.2	0.2	0.2
C_{22}	20.5	21.8	20.2	21.5
Other[a]	1.5	1.4	2.0	1.9

[a]Branched chain fatty acids.

The further complication arising from the chain length overlap on highly efficient polyester substrates is that a number of minor (probably from 0.1 up to 3% each) components will fall under other components. For example hexadecatrienoic acid may coincide with octadecanoic acid, hexadecatetraenoic acid may fall under octadecenoic acid, and arachidonic acid under docosenoic acid. For this reason the number of components listed is limited to those considered free

from this problem, or large enough that a small contribution from another component will not give a significant error. More extensive studies would be necessary to ensure complete separation of each acid. In common with other marine oils the probable number of components is of the order of fifty (Ackman *et al.*, 1962). The general analysis is comparable with herring oils examined in this laboratory under similar conditions, and to similar oils reported (Klenk and Eberhagen, 1962) in the literature.

The higher iodine value of the female capelin oil is in all probability due to the presence of highly unsaturated fatty acids in the eggs (cf. iodine value of salmon egg oil, Bailey 1952). The few percent increase in the proportion of eicosapentaenoic and docosahexaenoic acids in the female capelin oil (Table II) accounts for nearly all of the difference indicated by the iodine value, while some contribution from other minor acids not included in the tabulated data would make up the balance. In this connection sardine eggs have been shown to be relatively rich in arachidonic and other polyunsaturated acids in contrast to the composition of certain other fats present in sardines (Lasker and Theilacker, 1962). These authors also suggest that the egg fat composition is directly related to the dietary intake, although fat metabolism in the spawning period is more usually considered to involve utilization of depot fat. The higher proportion of C_{18} acids and the lower proportion of the eicosenoic and docosenoic acids is also probably consistent with that reported by Lovern for salmon egg lipids (Hilditch, 1956).

The synthesis of the highly unsaturated acids is usually considered to proceed from shorter chain precursors. Therefore the lower percentage of eicosenoic and docosenoic acids in the female capelin oil in contrast to the oil from male capelin is unlikely to arise from interconversion of the monoethenoid and polyethenoid acids of the same chain length (cf. Hilditch, 1956), but may be considered due to the overall changes in the fatty acid pattern.

REFERENCES

Ackman, R. G., R. D. Burgher and P. M. Jangaard. 1963. (In press.) Component fatty acids of seal oil: a preliminary survey through gas-liquid chromatography and urea complex fractionation *Canadian J. Biochem. Physiol.*

Andrews, G. L. 1954. *Fish. Res. Bd. Canada, Atl. Prog. Rept.*, No. 59, pp. 6–7.

Bailey, B. E. 1952. Marine oils, with particular reference to those of Canada. *Bull. Fish Res. Bd. Canada*, No. 89, pp. 325–326.

Hilditch, T. P. 1956. The chemical constitution of natural fats. 3rd ed. John Wiley and Sons, Inc., New York, pp. 49–51.

Horrocks, L. A., D. G. Cornwell and J. B. Brown. 1961. *J. Lipid Research*, **1**: 92–94.

Kaufmann, H. P., A. Seher and G. Mankel. 1962. *Fette, Seifen, Anstrichmittel*, **64**: 501–509.

Klenk, E., and D. Eberhagen. 1962. *Hoppe-Seylers Z. Physiol. Chem.*, **328**: 180–198.

Lasker, R., and Gail H. Theilacker. 1962. *J. Lipid Research*, **3**: 60–64.

LEIM, A. H., S. N. TIBBO, L. R. DAY, L. LAUZIER, R. W. TRITES, H. B. HACHEY AND W. B. BAILEY. 1957. Report of the Atlantic Herring Investigation Committee. *Bull. Fish. Res. Bd. Canada*, No. 111, pp. 177–184.

METCALFE, L. D., AND A. A. SCHMITZ. 1961. *Anal. Chem.*, **33**: 363–364.

MØLLER, D., AND S. OLSEN. 1962. *Fiskets Gang*, **48**(3): 27–36; or *Fisken og Havet* **1962**(1): 1–10.

PITT, T. K. 1958. *J. Fish. Res. Bd. Canada*, **15**: 275–293.

TEMPLEMAN, W. 1948a. The life history of the capelin (*Mallotus villosus* O. F. Müller) in Newfoundland waters. *Res. Bull. Newfoundland Govt. Lab.*, No. 17, pp. 33–62.

1948b. *Ibid.*, p. 38.

1948c. *Ibid.*, p. 12.

VANDENHEUVEL, F. A. 1952. *Anal. Chem.*, **24**: 847–851.

Effects of Artificial Propagation and the Weather on Recruitment in the Lake Ontario Whitefish Fishery[1,2]

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ABSTRACT

No significant relationship could be found between variations in the level of fry planting and ensuing variations in the level of catch in the long-term statistics of the Lake Ontario whitefish gill-net fishery. An alternate-year planting experiment in which fry were planted in the even-numbered years 1944 through 1954, similarly failed to show a detectable level of contribution of the hatchery fish to the fishery. The supported year-classes averaged larger than those not given hatchery support but this was judged coincidental because of a phasing with an alternate-year periodicity which characterized the catch statistics over the whole series examined, and was present in the six years prior to the start of the alternate-year plantings. Estimates of spawning stock were calculated and it was not found that the progeny-per-parent ratios were significantly affected by the fry plantings.

A possible explanation for the periodicity was suggested by a significant correlation between air temperatures at the times of spawning and hatching, and the strengths of the produced year-

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classes. Cold Novembers followed by warm Aprils appeared to provide conditions associated with the production of larger year-classes, with the opposite combinations relating to the weaker broods.

The disappearance of lake trout and ciscoes from the commercial catch resulted in increased fishing pressure directed towards the capture of the whitefish. Increases in the efficiency and intensity of the fishing were observed during the period of the study and these were likely responsible for the reduction of the average age of the fish in the catch by almost one year, and the resultant restriction of the annual catch to one year-class in recent years. Probably because most of the fish are currently caught before first spawning, a decline in spawning stock was almost continuous during the study period. The year-to-year fluctuations in the level of the catch increased both because of the reduced average age, and because of a greater variation in year-class strength. The year-classes produced in favourable years tended to increase, down to quite low levels of stock. This gave a configuration similar to Ricker's Type C reproduction curve, and which differed chiefly in that the limiting diagonal representing minimum reproduction fell below the replacement diagonal. It was suggested that the whitefish may require more than one spawning, to achieve stock replacement. The present instability of the catch, and the potentially serious effect of any sustained break in the rhythm of the climatic conditions suggest a condition of over-exploitation in this case.

INTRODUCTION

THE CANADIAN WATERS of Lake Ontario received hatchery plantings of whitefish (*Coregonus clupeaformis* (Mitchill)) fry in nearly all years between 1882 and 1954. The catch of the commercial fishery varied greatly from year to year in no apparent relation to the size of preceding plantings, and in spite of the plantings the peak catch years in the 1920 decade were followed by a steep downward trend which lasted for a number of years. Concern over this decline led in 1944 to the initiation of a study of the effectiveness of the fry plantings.

An experiment similar to that described by Miller (1946) was set up to permit study of the hatchery contribution to the fishery. The Glenora Provincial Fish Hatchery, on the Bay of Quinte (Fig. 1) near Picton, Ontario, had been the only source of whitefish fry for Lake Ontario for some years, and the operations of this station were placed on an alternate-year basis. The hatchery thus produced fry in the even-numbered years 1944 through 1954, and was inoperative in the odd-numbered years 1945 through 1953. No further plantings have been made since 1954.

Picton is the chief clearing centre for the Lake Ontario commercial fishery, and a convenient location for examination of the catch. A series of investigators have been stationed here each summer since 1944 to examine the commercial whitefish catch for possible effects of the alternate planting routine.

A preliminary report (Lapworth, 1956) summarized the data from 1944 through 1951, and examined the long-term catch statistics for the Bay of Quinte in relation to preceding levels of hatchery support. Age determination by examination of the scales indicated that five-year-old fish (five completed annuli) dominated the samples, contributing an average of 47% to the annual scale sample collections. Over the period 1924 through 1951 Lapworth was unable to find a correlation between numbers of fry planted in the various years, and the corresponding catches falling five years later when the plantings would have

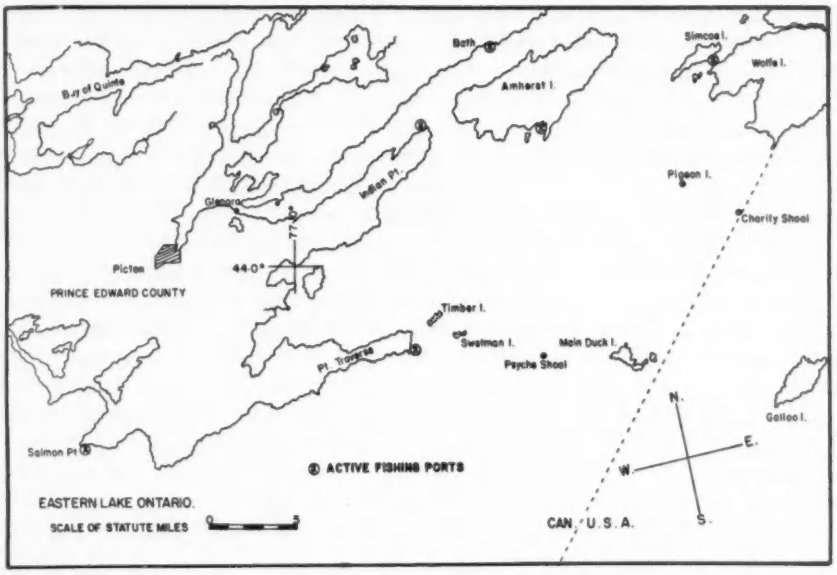

FIG. 1. Map of eastern Lake Ontario, showing the principal whitefish grounds, and important ports of landing.

been expected to have their greatest effects. Similarly, no correlation was demonstrable, when the catch values for 4 and 6 years following the plantings were used.

The age composition data for the period 1944 through 1951 applied to the appropriate total catch values (in terms of numbers of fish) permitted estimation of the total numbers of fish contributed to the fishery by the year-classes of 1940 through 1945 during their three principal years in the fishery. The range of variation in year-class strength was not great and the author showed that while the 1940 year-class was the strongest of the six, and received the heaviest hatchery support, the variations among the other year-classes appeared unrelated to their corresponding fry plantings.

The last year-class supported by a planting (1954) has essentially passed through the fishery, so that while future trends in the fishery in the absence of plantings altogether will provide the final test of current conclusions, the alternate-year planting experiment can be considered completed. The present work is an analysis of commercial catch sampling data collected since 1951, and a re-examination of the earlier material in the light of a different interpretation of the age of the Lake Ontario whitefish.

WHITEFISH GILL-NET FISHERY

Koelz (1926), referring to the Canadian fishery of Lake Ontario, pointed out that: "Since this date [1910] over two-thirds of all the netting on the lake

has been employed in a small sector to the eastward from Brighton"[2]. That this is still the case is reflected in the fact that more than one-half of the lake's total annual yield from all commercially exploited fish stocks (currently averaging about 2 million lb per year) is shipped to the markets from the town of Picton (see Fig. 1) alone.

The line of shoals and islands to be seen in Fig. 1 running eastward from Point Traverse through Main Duck and Galloo Islands to the United States shore separates what will be referred to here as the "eastern basin" from the remainder of the lake. Lake Ontario has a generally deep basin with steep shores. As Koelz (1926) noted, the 30-fathom depth contour around most of the lake averages only 5–10 miles from shore on the north side and three or fewer on the south. Within the eastern basin however, depths seldom exceed 20 fathoms, and this fact undoubtedly bears on the concentration of the commercial catch in this area.

The inshore fisheries, using various gill-net mesh sizes, hoop nets and baited hooks, take bullheads (*Ictalurus nebulosus* (Le Sueur)), American smelt (*Osmerus mordax* (Mitchill)), carp (*Cyprinus carpio* Linnaeus), several Centrarchids, American eel (*Anguilla rostrata* (Le Sueur)) and yellow pickerel or walleye (*Stizostedion vitreum vitreum* (Mitchill)). These species are caught within the Bay of Quinte and the various shallow bays along the Lake Ontario shore of Prince Edward County. Their importance to the fishery has increased greatly in recent years with the decline in the abundance of the preferred offshore species.

The principal offshore grounds for the whitefish catch are mainly within the triangular area whose apex is the head of the bay (Prince Edward Bay) between Indian Point and Point Traverse, and whose base is a line drawn northward from Main Duck Island to Amherst Island. The two headlands mentioned above are the main ports of landing for the whitefish catch, and the other ports shown in Fig. 1 are each used by only one or two boats.

The areas of the Bay of Quinte lying to the north and west of Glenora have always been the principal spawning and nursery grounds for the whitefish. Spawning takes place in November and the fishery is concentrated here from the beginning of October until the freeze-up in December. Many of the year-round commercial fishermen participate, but this fishing is carried out predominantly by farmers and others who operate for the short period only. The fishery is greatly dispersed at this time with most of the fishermen operating from individual landings. A few less extensive spawning shoals outside the Bay of Quinte are also fished for whitefish in the fall.

Whitefish, lake trout (*Salvelinus namaycush* (Walbaum)) and the ciscoes (*Leucichthys* sp.[3]) made up the bulk of the Canadian Lake Ontario catch until comparatively recently but of these only the whitefish now remains in commercial abundance. There was no year between 1914 and 1927 when the aggregate catch for the lake fell below 4 million lb, and the great abundance of the cold-

[2]Situated on the north shore immediately to the west of the Prince Edward County penninsula (Fig. 1).

[3]*Leucichthys* = *Coregonus* according to the "List of Common and Scientific Names of Fishes from the United States and Canada". Am. Fish. Soc. Spec. Pub. No. 2, 1960.

water forms was mainly responsible. After that time, the trout and whitefish catches receded steadily and the commercially less valuable ciscoes were relied on more heavily to sustain the offshore catch. Of the 17 years between 1928 and 1944, only 6 of the annual catches of ciscoes were below 1 million lb, and the average was 1.25 million lb per year. This support failed after 1944, however, and the annual cisco landings declined to (apparently) permanent insignificance in a matter of a few years.

For the 1928 to 1944 period the whitefish catch averaged 527,000 lb and the trout catch 250,000 lb per year. The decline of the lake trout catch, however, was continuous from 1925 with only minor interruptions. There were no annual catches greater than 50,000 lb after 1947, and the latter years of the 1950 decade saw virtually no trout taken other than the survivors from various experimental introductions.

The decline in the offshore catch resulted in a gradual decrease in the size of the fishery, but the remaining fishermen have increased the intensity of their exploitation of the whitefish substantially during the period of this investigation. This has been largely possible through improvements in their efficiency.

The open-water fishing fleet formerly consisted almost entirely of open, wooden-hulled motor launches ranging in length from 20 to 40 feet and powered by automobile engines. Around 1951 the enclosed fishing tug began to make its appearance in numbers, and at the present time most of the lake whitefishing is done by a fleet of about 10 enclosed and 4 semi-enclosed tugs varying between 30 and 45 feet in length. All but one of the enclosed tugs are steel-hulled and a change-over to diesel power is well under way. A few have recently installed sonar equipment, but as yet only one boat is radio-equipped. The simple, locally constructed net-lifting "gurdies" similar to those described by Smith (1961) have given way in these boats to the faster mechanical net-lifters. The tugs are capable of handling more gill-netting in a day than the open boats, have a greater range and are far less hampered by poor weather conditions. The small, open boats are still used for the fall spawning-run fishing in the Bay of Quinte.

The standard catching gear is the 4½-inch mesh (extension measure) gill-net. Until 1950 linen gill-nets had been the principal whitefish gear, but when the nylon nets became available the change-over to this more efficient netting was almost immediate.

Cotton and linen gill-nets require a great deal more handling than do the nylon nets. Formerly, the nets were spread full width on reels for drying, and when ready for fishing again they were placed on smaller 4-bladed reels called "spools". For setting, the spool was mounted across the stern and the nets paid out as the boat moved ahead. The fishermen now set directly from trays in which the nylon nets are coiled with the sidelines and netting drawn together in the "rope". For the less frequent dryings the nets are also wound rope-fashion on the reels except when fouled or damaged. This has not only greatly reduced the net-handling time, but has permitted more nets to be carried, since the trays occupy less deck space.

The basic unit of gill-netting is the pound of twine. The nets are usually hung in 2 or 3 pound units and fished from net trays (boxes) containing 6 lb. The length of netting in a tray varies between 400 and 500 yards and this was also approximately the length range of the spools. Fishermen now commonly lift and reset from 15 to 20 trays of gill-netting in one day whereas 5 or 6 nine-pound spools was formerly about the limit in the smaller boats.

Since the advent of the nylon material, the nets have become progressively wider and of finer thread. In the open lake fishery approximately 60% of the nets now in use span the legal maximum 36 meshes in width. When fishing, these nets measure about 12.4 feet between float and lead lines. This is approximately twice the fishing width of the linen nets. The 30-mesh width was the most popular for several years and roughly 20% of the nets are still of this width. The remainder of the nets are narrower and are generally used for fishing the shallower waters in the fall.

It is estimated that in recent years the meshes have averaged about 4.1 inches in the vertical axis by 1.8 inches in the horizontal while fishing. However, the fishermen prefer to maintain about the same overall length per net, and there has been a tendency to shirr the netting on the sidelines as the finer (and thus lighter) nylon netting has become available. A limit is apparently being reached currently however, because the finest available twines are not proving sufficiently durable. With the fixed weight of netting in a tray and the tendency to compensate by shirring for gains in length obtained with the lighter gill-netting materials, the area of a tray of gill-netting (about 1500 sq yd) has probably not changed radically since nylon gill-netting became available. The much coarser linen nets covered appreciably smaller areas, however, than comparable units of the lighter nylon netting.

Evidence will be presented to show that the impact of the more efficient netting and the increased intensity of the fishing operations brought about a sharp reduction in the average age of the whitefish composing the catch. The stock is now fished essentially one year-class at a time. Further, it will be shown that there was only a very minor increase in the total number of fish harvested from the recent year-classes, and that the stability of the fishery has declined demonstrably during the course of this study. At present the life of the whitefish fishery appears even more intimately dependent on the vagaries of reproductive success than it was in the early years of the investigation.

MATERIALS AND METHODS

Statistical Sources

Whitefish commercial catch statistics[4] have been assembled from several sources in a single volume entitled "The Canadian Commercial Fisheries of the Great Lakes" (Canada Dept. of Fisheries — Basebook on Fishery Statistics — No. 2, 1955). The total landings for the years 1867 to 1951 (in cwt) were taken from this source. The totals for the various areas of Lake Ontario for all years and the grand totals for the years 1952 to 1960 were obtained directly from the

[4]Only Canadian catch statistics are considered since American landings have been negligible.

Annual Reports of the Ontario Dept. of Game and Fisheries and its successor (after 1946), the Fish and Wildlife Branch of the Ontario Dept. of Lands and Forests. Table I lists the annual landings of whitefish from Lake Ontario for the years 1924 to 1960 in column 3. The annual contributions of the Bay of Quinte are shown in column 1. Column 2 lists the landings for all Canadian waters, including the Bay of Quinte, eastward from Brighton to the St. Lawrence River. The difference between column 3 and column 2 for each year represents the whitefish harvest of all the fisheries westward from Brighton. These values vary in roughly parallel fashion with those for the eastern basin, and average only 16% of their corresponding lake total values. On this account it was felt that no serious error would be introduced into the analyses by the use of the total values of column 3.

The numbers of whitefish fry planted in the Bay of Quinte each year were summarized from the Ontario Government records by Lapworth (unpublished data) and these values appear in Table II. Small plantings were made in nearly every year of hatchery operation in other areas of the lake, but they represented very small percentages of the annual totals, and were not added to the Lapworth figures. Some of the records of whitefish culture before this became a provincial responsibility were obtained from the Annual Reports of the Dept. of Marine and Fisheries (Canada).

Records for daily spawn-arrivals at the Glenora Hatchery from the pound-net operations in the Bay of Quinte were available for some years in the Glenora Hatchery files and these will be referred to later in this account.

Local weather observations for the years 1924 through 1957 were made at Belleville, and these included the air temperature data summarized in Table X. Earlier (1915–23) air temperature data are also referred to, and these were recorded at a station in Bloomfield. The records for the stations were read from the monthly summaries of the Meteorological Branch, Canada Department of Transport.

Sampling the Commercial Catch

Investigators stationed at Picton each summer attempted to examine a sample of fish representative of the age and size composition of the total commercial catch.

The routine described by Lapworth (1956) remained essentially unchanged throughout the study. During each summer daily trips were made to the fisheries, where the fishermen were interviewed for information concerning the nature and location of the fishing effort. The selection of catches for examination was not random owing to the small number of fishermen involved. The practice was to deal with the fishermen in rotation, attempting to obtain equal representation from each man within a season's sample. However, the working schedules of some of the fishermen were such that in some cases their catches were available but the fisherman seldom seen, and with others late landing or sale of the fish outside Prince Edward County prevented both examination of the catch and the interview. As a result, it often happened that the rotation was restricted to only three or four operators for long periods.

The examination of the fish was carried out on return to the fish-buyer's warehouse in Picton before the fish were packed for shipment. Throughout the study it was the practice to examine all the fish in a catch where possible, excepting only those which had drowned in the nets and were eviscerated when landed, and the small numbers taken for the table by the fishermen or sold at the fisheries. The length of each fish was measured to the fork of the tail, always taken to the lower one-quarter inch interval. Weights were measured on fish "in the round" (they are not normally eviscerated for the market), in pounds and ounces. Scale samples were usually taken from the left side of the fish in the area immediately ventral to the leading edge of the dorsal fin.

Table III summarizes the data collection. The number of fish examined (which is only slightly greater than the number of specimens for which ages were determined) ran slightly lower in the earlier years because the work was largely confined to the four months June through September. Since 1954 the May catch has been sampled each year as well. In addition, samples were collected from the commercial catch during all but two months of the period May 1956 through December 1958.

The collection has averaged about 1800 scale samples for the June through September period, and ranged from 1200 to 3300 per year. The proportion of the total catch included in each summer's examinations is shown in Table III. Each monthly total reported whitefish catch in pounds was converted to an estimate of the total in terms of numbers by dividing by the respective monthly weight average for the fish in the samples. The sums of the four values thus derived for each summer appear in the third column of Table III. The period 1944 through 1947 is not included because the catch values were not summarized on a monthly basis prior to 1948. The summer fish examinations have represented from 2.1 to 5.0% of their corresponding catch totals with an average of 3.4%. Generally at low catch levels more individual catches are sampled. The fraction of the total catch which can be examined by a single investigator increases therefore, with decreasing levels of catch, to a point where the numbers of available fish become limiting. Examination of 5% of the total number of fish caught in the summer period is probably close to a maximum under the present circumstances.

Prior to 1954, only the catches of the Indian Point Fishery were included in the sampling. It was felt that possible racial differences between the stocks exploited by this and the more important Point Traverse fishery might act to mask the effects of the fry plantings, which were preponderantly made within the Bay of Quinte. The whitefish catch reached a low level in 1953 and 1954 however, and the Indian Point fishery frequently turned to inshore fishing for other species and could not be relied on for daily catch sampling. By 1955 the Point Traverse fishery therefore had become the principal source of whitefish samples. Comparisons of the age composition of samples from the two fisheries failed to reveal significant differences. For example, in May 1954, three Point Traverse and two Indian Point catches were examined and the frequencies for the 181 age determinations were as follows:

Age	*Point Traverse*	*Indian Point*
III	13	6
IV	28	21
V	27	13
VI	27	16
VII	10	6
VIII	3	1
Total:	118	63

The Chi^2 for these distributions is 0.53 with 5 degrees of freedom. Further evidence that the fisheries exploit a common stock over the whole of the eastern basin came from the broad summer distribution of tag returns from fish marked within the Bay of Quinte at the time of spawning.

Studies of Whitefish Spawning

Hay Bay is the long (11 miles) narrow bay running in a southwesterly direction, which joins the Bay of Quinte proper at a point 3 miles north of Glenora (see Fig. 1). This has been known as one of the principal areas of whitefish spawning for many years, and the Glenora Hatchery spawn-taking operations were centred here. A tagging program was started in the fall of 1953 in conjunction with the last spawn-taking, and a trapnet has been set for tagging purposes at the same location each November since.

Data on the age, size and sex composition have been collected for the fish captured each fall. These observations are summarized in Table XI for the years 1953 through 1958. In general, the net was set in late October each year and fished until the freeze-up, so that the spawning run at that location was sampled during its whole duration.

At various times gravid female whitefish were sacrificed for fecundity analysis, and these results will also be discussed in a later section.

AGE DETERMINATION

The present interpretation of the age of the whitefish as recorded on the scales disagrees with that of Lapworth (1956). All the early scale samples were re-examined, and the new readings on a number of collections since 1944 set age IV rather than age V as the predominating group. Of even greater importance however, is the fact that the largest year-class now appears in the order of twenty times the size of the smallest.

Lapworth's (1956) age determinations were at variance with those of E. J. Hamley, who carried out the first four years of the investigation. The average lengths at each age calculated by these workers for the periods 1944–47 and 1948–51 are reproduced in Fig. 2 from Lapworth's fig. 4, and compared with averages calculated from the recent age determinations for the period 1944–51. The recent scale interpretations are essentially in agreement with those of Hamley.

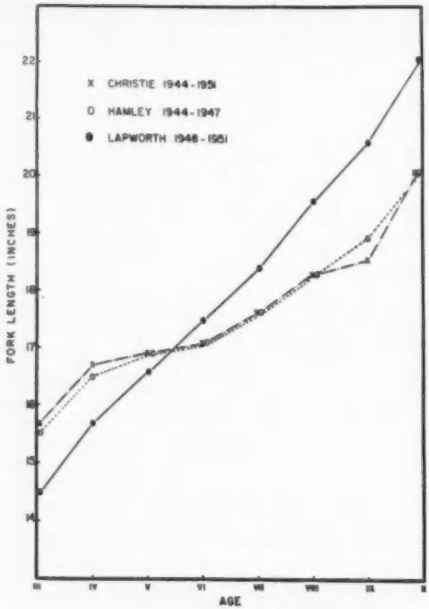

FIG. 2. Comparison of age–length relations computed from three interpretations of the scales of the Lake Ontario whitefish.

Not much can be inferred from Fig. 2 about the growth rate of the whitefish. The Lake Ontario whitefish have a girth-to-length relationship which is very similar (Christie, unpublished) to that described by McCombie and Fry (1960) for the South Bay, Lake Huron whitefish, and in that case the modal fork length indicated for a 4½-inch mesh gill-net was 18.5 inches. Very few Lake Ontario whitefish survive to this size, and the curve is probably the resultant of mesh selection and selective mortality, respectively acting to bias the lower end of the curve upwards and the upper end downwards.

Age determinations throughout the work have been made from impressions of the scales in cellulose acetate slides. The early readings were made with small microprojectors and the more recent by the use of the "Van Oosten" (Van Oosten *et al.*, 1934) type of projector, at a somewhat greater magnification (40 diameters).

In the recent work, from ten to fifteen scales were pressed on a single slide using a pneumatic scale press (Baker and Brohm, 1960). Ages were assigned without reference to the length of the fish and a second reading was made without reference to the first. When differences were encountered between readings, the scales were scrutinized further, and a decision reached. Ages were assigned in all cases except those where only regenerated scales were included in the sample.

The incubation of whitefish eggs requires most of the winter, and the hatching usually takes place in April. The age of the fish refers to the year of hatching and is always given as the number of completed annuli counted, expressed in roman numerals. By convention, January 1st is designated as the birthday of all the whitefish.

The criteria used in the identification of an annulus in the present work are basically as follows: "cuttings-over" (Hile, 1941) are nearly always associated with annuli in this stock, and this was the primary characteristic looked for in the recent determinations. The heavier first circulus of the new year's growth is particularly distinct in the posterior quadrant and this was a useful secondary characteristic. To be judged valid, an annulus had to appear on both dorsal and ventral aspects of a single scale and on all scales in the sample. Most marks discarded as false annuli were growth discontinuities which lacked both cuttings-over and consistency. Sometimes they were clearly "dislocations", (Van Oosten, 1929) or other anomalous markings which matched the diameters of scale regenerations, and were undoubtedly formed at times of injuries.

The frequency of scale replacement is apparently high and the marks formed on scales elsewhere on the fish at these times may have, in a few cases, been confused with true year marks. In making the impressions no attempt was made to discard regenerated scales. A study of samples from 200 fish taken in August 1948 revealed that 111 (54.5%) contained at least one regenerated scale. Altogether the lot included 2449 scale impressions with a total of 220 regenerated scales (9.0%). Where false annuli were formed in connection with such traumata, there was considerable variation noted in their distinctness. A small proportion may have satisfied the criteria for true annuli, therefore, and passed undetected.

In the recent work it has not been found that bands of crowded circuli are reliable winter marks unless cuttings-over are also present. As Van Oosten (1929) pointed out, the crowdings often indicate interruptions or changes in growth rate during the summer. The most common location for such markings in the Lake Ontario whitefish scales is inside the first annulus, and the band is more distinct in younger fish.

At various times three scale readers worked with the author on this large collection of scales. During one summer period all three worked on the collections, and several tests were given them on samples of unidentified scales. For these the readers were required to work separately, and the only information given them was the season of the collection. Good agreement resulted in all cases. For example, the last test gave the same ages for 113 (78%) out of 145 samples and, aside from the general difficulty with extreme ages, no clear trend could be seen in the differences.

No independent test of the validity of the age determinations is available at this time, but the application of the data provides substantive evidence. It will be noticed in Table V, for example, that there is strong between-year consistency in the representation of various year classes in the catch. Figure 4 illustrates the normal consistency in age distribution among samples drawn within the same year.

YEAR-CLASS COMPOSITION OF THE WHITEFISH CATCHES

As previously indicated, the whitefish sampling program has only been continuous for the months June through September during all years. Since the age composition data are used to calculate annual yield by age, a brief consideration of their representativeness is necessary.

Figure 3 shows the seasonal cycle of whitefish catches expressed as percentages of the annual landings and averaged for the years 1948–60. There are three distinct fishing periods in the year. In the spring (Jan.–May), the nets are set in less than 15 fathoms depth and catches reach a peak in April. By the end of May, the fleet has moved offshore to fish in depths between 15 and 25 fathoms. By the end of September, another inshore phase begins, culminating with the November spawning-run fishing which contributes the highest monthly fraction of the annual catch (16.6%).

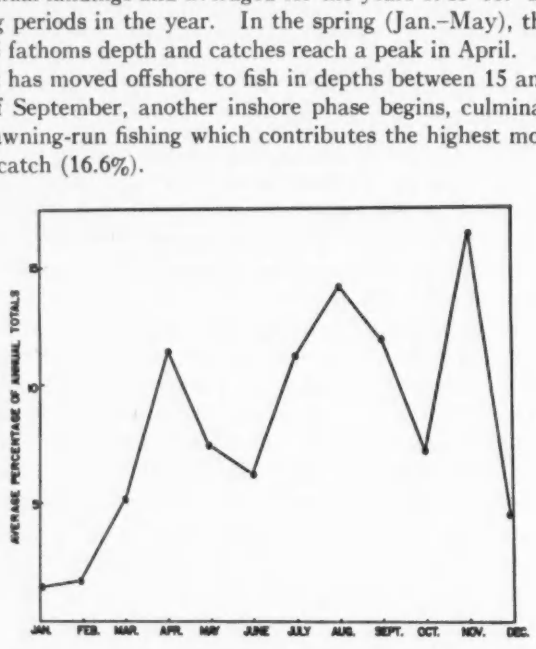

FIG. 3. The annual whitefish catch cycle. Values are average (1948–1960) percentages of the annual total catch, by month.

The percentage contributions of the summer (June–Sept.) catch (in pounds) to the annual totals are shown for each year from 1949–60 in the last column of Table I. The 1950 value is unusually high and this is attributed to a "fishing-up" effect which will be discussed later.

There is a great deal of variation about the average (41.8%) and it is felt that while the summer catch is influenced by such things as the weather and market conditions, the chief source of this variation lies with the relative strengths of the recruiting year-classes. The recruiting year-classes swell the late summer catch but contribute little to the spawning run catches. Thus, in a year of low recruitment, essentially the same stock is fished around the year. The concentration of the spawning fish, therefore, makes the fall catch proportionately greater, and the summer catch relatively smaller.

Sampling was carried out during each month of the year for the first time in 1958. The age composition percentages for the monthly samples are shown in the histograms of Fig. 4 to illustrate the relation between the catch changes and variations in the age composition. An increase is normal in the representation of three-year-old fish in the catch of the offshore fishery through the summer, but it is particularly pronounced in this case because of the strength of the 1955 year-class. The November catch consists principally of spawning fish taken within the Bay of Quinte, and the proportion of three-year-old fish drops during that month. Spring catches characteristically contain higher proportions of three-year-olds than the early summer catches, and this was also the case in 1958. While this is often a good indicator of the strength of the year-class to be recruited later in the year, the age III catch in spring is always small compared with the late summer catch, when the fish have grown to a size more vulnerable to the nets.

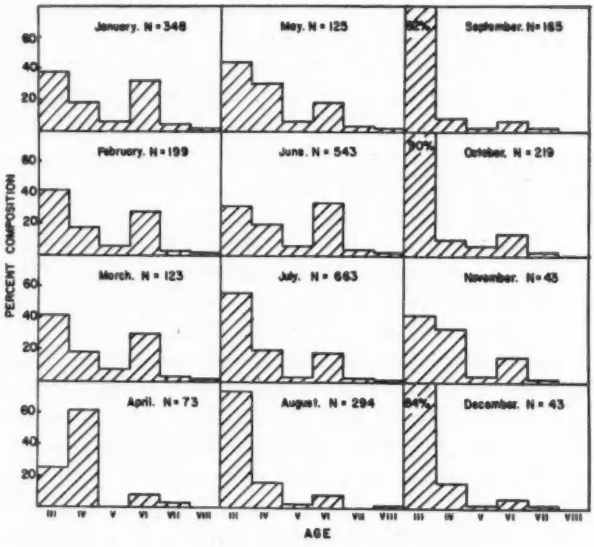

FIG. 4. Monthly age frequency histograms from the 1958 scale sample collection.

The stability of the age composition polygons for the more vulnerable age groups is apparent in Fig. 4. This was tested statistically for the ages V, VI and VII. The data were arranged by month in a contingency table (3 × 12) and tested for independence following Snedecor (1956, p. 226). The sum of the Chi-squares for 22 degrees of freedom was 32.41. This gives a probability just over 0.05 which indicates a difference between observed and expected frequencies which is just on the borderline of significance. It was noticed that the greatest deviations from the theoretical frequencies occurred in the months February and October, and in particular within the age V group. The test was repeated with

the data for these two months deleted, and the new sum of the Chi-squares was 16.8 with 18 degrees of freedom. This reflected a probability greater than 0.5 indicating that the differences had fallen well below the level of statistical significance. The 1953 year-class was poorly represented in all months, and it seems quite doubtful that anything more than sampling error was involved in the deviations of the two months. On the strength of the data for 10 months, therefore, it was taken that departures from the ratio for these ages during the year, for our purposes were random. It is interesting that there were no trends in the departures from the theoretical ratio between the ages tested. This may indicate that fish of these ages are subject to similar mortality rates within the year.

The foregoing suggests that samples representative of the older fish catches may be drawn at any time of the year, but representative catch estimates for ages III and IV should be prepared from the age composition of spring and fall samples (when no growth is taking place) and for each month of the summer period. The error introduced by the use of summer data only does not appear to have been great however. For example, the estimate of the yield from the 1955 year-class prepared from the 12 monthly samplings in 1958 exceeded the estimate based on the summer percentage (Table IV) representation used with the annual catch total by only 10%, and this is likely near the maximum.

For each year the four monthly percentages for any age were weighted by the various monthly catch totals (in numbers). As mentioned earlier, total catch data were not collected on a monthly basis prior to 1948, so the average monthly catch percentages for the later period were used as weights for the earlier data. The weighted percent age composition estimates are found in Table IV. The samples of recent years have contained very small numbers of age II fish at times, and these have not been included in the Table.

The proportions of older fish in the samples are markedly reduced in the collections of the recent years. The average age values listed to the right in the Table dropped from the 1944–49 average of 5.18 years to 4.29 years through the 1950 to 1960 period. Years in which recruitment was low in general gave higher average age values, but in only one year (1953) of the last 11 did the average exceed the lowest value for the first six years.

Appreciable changes in the size composition accompanied the reduction in average age. Figure 5 illustrates this. In the samples for the summers of 1944 through 1949 the percentages of whitefish less than the 2 pound legal minimum weight averaged 8.6, but since 1950 the average has been 23.9. In the latter period, the agreement between the peaks of high production of undersized fish and the representation of age III recruits in the catch has been generally good, in spite of variations in fishing intensity and growth. The year 1950 was exceptional for the probable reason that the 1946 year-class was fished extensively for the first time at age IV, before the fish had attained appreciable growth. It seems most probable that the sharp change in the age and size composition following 1950 was due to the introduction of the nylon nets and it is taken in all ensuing discussion that this effect and the associated reduction in the stock of older fish were strictly fishery-induced.

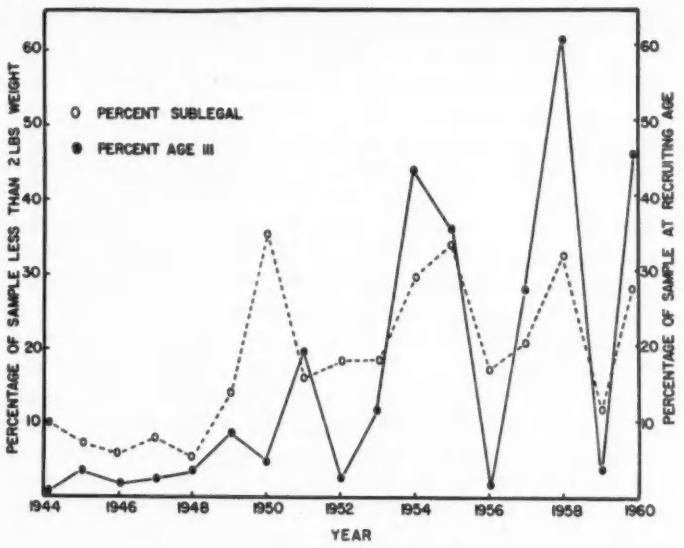

FIG. 5. Recruitment effects in the Lake Ontario whitefish fishery. Sub-legal percentages are from numbers of fish < 2 lb in weight in the samples of June through September.

McCombie and Fry (1960) showed that cotton and nylon gill-nets had essentially the same selection properties, but that the fishing power of the nylon was greater. The ratio of their nylon-to-cotton whitefish catches was 2.9:1, and it is noteworthy that a very similar increase of 2.8:1 in the proportion of undersized fish is indicated by these data. There is little doubt that this sharp response to the more efficient gear is indicative of the high rate of exploitation in the fishery—a fact which has been substantiated in recent years by a high rate of tag return.

To calculate the catch by age, the catch totals of Table I were divided by average weight values which were also derived from production-weighted monthly averages. These estimates of the numbers of fish caught are seen in the right-hand column of Table V, and for each year they are segregated by the age composition percentages into estimates of the numbers caught from each year-class.

Estimates of the minimum initial strengths of the year-classes have been prepared from Table V using the "virtual population" method of Fry (1949). The estimates can be seen in Table VI. These are the simple sums of the numbers of fish caught from each year-class at each age in the fishery. As an example of the development the 1941 year-class first entered the fishery in 1944 at age III and its contribution in that year was estimated at 5756 fish. The following year it contributed 9508, and so on, reading diagonally downwards and to the right in Table V. The sum of all the contributions (43,190) is the first entry in Table VI for this year-class, and represents the minimum number of fish of the

brood present at the beginning of age III. The next entry for the year-class is 37,434 and this is the minimum total following the removal of the age III catch.

In this fishery year-classes have made their major contributions before age VII and are rarely seen at ages greater than X. The 10 year-classes 1941 through 1950 have had complete passage through age X in the fishery. In addition, the year-classes 1951 through 1954 can be added to the series without unduly affecting the total by summing contributions for each year-class through age VI. For example, the 1941 year-class entered the fishery at age III in 1944. Its contributions at ages III, IV, V and VI estimated in Table X are 5756, 9508, 14,681 and 6176. These sum to 36,121 fish, and this is the entry for this year-class in Table VII.

Estimates of the sizes of the three year-classes preceding and the three following the 1941 to 1954 series have been calculated from the incomplete contributions seen in Table V. The 14 complete year-classes gave average contributions to their respective totals as 15.1% at age III, 47.4% at age IV, 28.1% at age V and 9.4% at age VI. For example, the observed contribution of the 1938 year-class in Table V is 22,297, and taking this as 9.4% of the total contributed by the end of 1944, the estimate 237,202 was computed, and appears in brackets in Table VII.

Virtual populations can only be considered unbiased estimates of relative year-class strength if the rates of fishing and natural mortality are steady. In this case the 1950 change in netting effected a sharp change in fishing mortality, and subsequent changes may have increased fishing mortality further. Depending on the magnitude of the rate of natural death in the stock (Bishop, 1959) therefore, the trend will be for the estimates for the early year-classes (1938–42) to be relatively too low and those for the year-classes 1943 through 1946 to increase towards the estimates made for the later year-classes.

It is interesting, however, that the strengths of the year-classes show little trend. The average contribution of the 9 year-classes 1938 through 1946 was 144,712 fish, and that for the 11 year-classes 1947 through 1957 was 150,516. This represents an increase of only 4% and it is not likely that this is significant. Considering the sharp reduction in average age likely induced by the introduction of nylon nets, a substantial gain in the harvest might have been anticipated from recent year-classes, had the rate of natural mortality been high relative to that of fishing mortality. A reduction in average reproductive success in the more recent period could have acted to reduce any gain through the capture of fish which otherwise might have been lost to natural mortality, but the apparent relationship between weather and year-class strength which will be discussed later, shows no trend which would support this.

The more intensive fishing actually effected a reduction in the annual poundage of fish taken. Even though the numbers of fish caught were roughly equal for the two periods, the average weight of the fish was lower for the 1950 decade (2.24 lb) than for the 1944–49 period (2.41 lb). This caused a reduction of 5.9% in the average catch (Table I) in the 1950 decade, compared with the annual landings of the 1940 decade. As might be expected the heavier fishing also had

the effect of increasing the amplitude of the year-to-year catch fluctuations. There was an increase of 10% in the coefficient of variation about the 1950 decade mean catch compared with that for the 1940 decade.

RESPONSE OF THE WHITEFISH CATCH TO PRECEDING FRY PLANTING

Historical

The artificial propagation of Lake Ontario whitefish was started in 1882 and by that time the first downward trend in the catch was well established. The planting record is not complete for all the years prior to 1920, but those data which have been examined suggest that the level of hatchery support was relatively quite low. In the period 1909 to 1915 for example, eggs from the Bay of Quinte were being hatched at Sarnia and elsewhere for distribution in other areas of the Great Lakes. The Reports of the Dept. of Marine and Fisheries (Canada) recorded only 6 millions of fry planted in Lake Ontario for each of the three years 1910, 1911 and 1912, and 4 millions in each of the two years 1913 and 1914. The distribution in Lake Ontario increased sharply with the establishment of the Thurlow Hatchery at Belleville, and the records show plantings of 45 millions in 1915 and 59 millions in both 1916 and 1917. The plantings continued to increase to a peak with the 1927 stocking of 208 millions of fry, and the general average for the 1920 decade was extremely high. After this period the plantings declined in size. The Glenora Hatchery was set up in 1922 and from then until 1936, both Bay of Quinte hatcheries stocked the Lake Ontario waters. Presumably the low spawn-take in the later years was a factor in the suspension of the Thurlow operations.

The annual catch totals rose from the all-time low value (79,000 lb) in 1902 to a peak (1,150,000 lb) in 1909, and then receded until 1913 (520,000 lb). Nearly every year from then until the 1924 catch peak (2,650,000 lb) was reached showed a sharp increase over the year preceding. This suggests that an increase in the abundance was under way after 1913, while the heavier plantings which started in 1915 could not have had any effect on the stock much before 1919. It is significant also that the heavy annual plantings continued a few years after the catch peak and apparently did not have sufficient influence on the catch to alter the steep downward trend. It is not likely, for example, that the fish from the enormous 1927 planting entered the fishery later than 1933 (age VI) and the period 1932 through 1934 marked the nadir of that catch period.

Figure 6 gives a comparison of values for the total spawn-take at the Glenora pound nets in 15 seasons with the corresponding total commercial catch values. The old hatchery files were not complete, and the data for the years not shown in Fig. 6 could not be located. The sharp reduction in the availability of spawn in the recent years of low whitefish abundance is clear. The relation between fry plantings and the preceding levels of catch has the same characteristic, but the variance is somewhat greater because of the suspension of the Thurlow operations and the fact that some fry were taken to other lakes for planting in certain years.

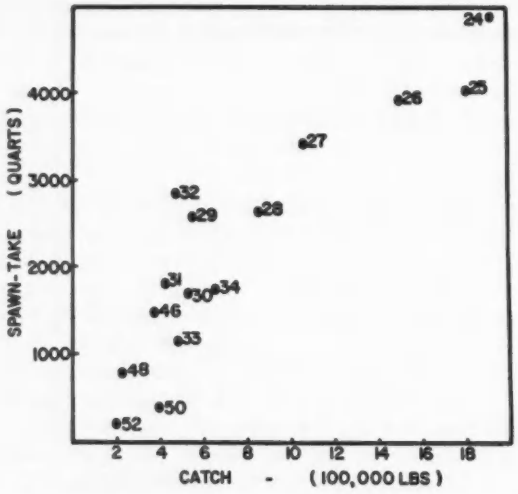

FIG. 6. Comparison of total annual Glenora Hatchery spawn-take with contemporary catch levels.

In summary, while there is little question that the abundance levels influenced the size of the fry plantings, there is nothing in the long-term catch statistics which would suggest that they had any significant dependence on preceding levels of fry plantings.

Figure 7 outlines the long-term trends in the whitefish catch. The ten-year averages with their respective ranges are also seen in Table VIII. The catch is not a simple function of abundance, but it is probable that the broad averages give a fairly accurate representation. Following a decline from the 1860's (the earliest available records) to the turn of the century, the annual catches increased to a great peak in the 1920 decade. The 1930 decade saw an extreme reduction in the level of catch. As pointed out in the last section, the decrease between the 1940 and 1950 averages is referable to the smaller size of fish taken in the recent period, and no change in the numerical size of the catch was noted.

Shown also in Fig. 7 and in Table VIII are similar decade average and range values for the lake trout landings. The catches of both species reached their all-time peaks in 1924, and Fig. 7 shows the great similarity in the abundance trends. The principal difference is that the native lake trout approached extinction (as a commercial product) during the 1950 decade, while the whitefish catches persisted. The lake trout catch was largely independent of the whitefish catch because larger mesh gill-nets were normally used for its capture. In addition, the trout was a preferred catch because it generally commanded higher prices and steadier market demand, so there is little doubt that the paralleling of the catch levels indicated similar changes in abundance.

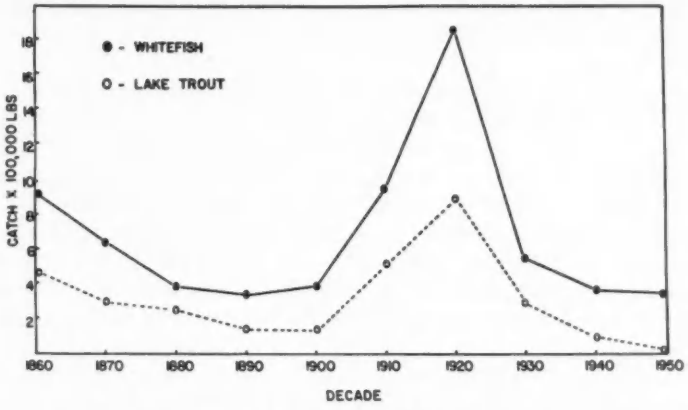

FIG. 7. Long-term trends in the Lake Ontario whitefish and lake trout catches. Values are averages for 10-year periods.

It is of interest also that the abundance of the burbot or ling (*Lota lota* (Linnaeus)), another cold-water form, may have also paralleled that of the whitefish. As the species normally has no market value, no catch records were kept to indicate the exact catch levels in the offshore gill-net fishery. Commercial fishermen indicate, however, that its occurrence in the contemporary commercial catch is extremely rare, and that it has declined steadily along with the lake trout since the early 1930's. Dymond *et al.* (1929) described very large catches of burbot in 1928 and 1929, and pointed out that "The ling are so abundant as to interfere seriously with the operation of the commercial fishermen at certain seasons of the year, particularly in the later winter and early spring". This was in particular reference to the western end of Lake Ontario. Of equal significance is their reference to an earlier period of low burbot abundance: "Mr. Robert Montgomery of Toronto, who fished with his brothers for ciscoes, whitefish and trout off Fisherman's Island, Toronto, between 1885 and 1892 never saw a ling during those years." The enormous abundance of burbot in the eastern basin during the 1920's is still spoken of commonly, and some of the older fishermen recall that the burbot were scarce in this area also during the period of low whitefish abundance at the turn of the century. It seems likely, therefore, that there was only one major peak of burbot abundance after 1900, and this coincided with the peaks for whitefish and trout.

It cannot be argued that the abundance levels of the two large piscivores depended on the abundance of the whitefish. Smith (1892) and Dymond (1928) both mentioned the alewife (*Alosa pseudoharengus* (Wilson)) as the principal food of the Lake Ontario lake trout and made no mention of predation on the whitefish by trout. Recently, examination of the stomachs of 2519 young trout recaptured between 1956 and 1960 from various experimental plantings identified

sculpins (*Cottus* sp., and *Myoxocephalus quadricornis* (Linnaeus)), alewife and smelt (in that order) as the three most important food types, again with no whitefish noted.

The alewife has also been cited as the chief food of the burbot by Pritchard (1929), and by commercial fishermen who recall commonly catching burbot which had attempted to eat already enmeshed alewife, and which they could partly swallow but could not disgorge because of the sharp abdominal scutes of the small fish. It would not appear then that the lake trout and burbot were exclusively or even significantly dependent on the whitefish for forage, so the paralleling of the lake trout and burbot catch trends with those of the whitefish cannot be attributed to predator-prey relations. The probability also seems the stronger for the fact that the whitefish persisted after the disappearance of the other two.

It is further unlikely that fish culture was involved in the paralleling because the burbot never received hatchery support, and the propagation practices differed quantitatively and qualitatively between the whitefish and trout. The trout spawn was obtained from the Lake Ontario stock, as in the case of the whitefish, but plantings were less intensive and were usually made as eyed eggs, sac fry, or advanced alevins on the exposed lake shoals of eastern Lake Ontario. The whitefish on the other hand were generally stocked as sac fry and largely in the sheltered areas of the Bay of Quinte.

The possibility that the abundance peaks of the three cold-water species were quite unrelated in origin cannot be dismissed, of course. The more tenable hypothesis, however would appear to be that the abundance levels shifted simultaneously in all three species in common response to some changes in the environment.

Analysis of Whitefish Commercial Catch and Planting Statistics

The considerations of this section were dealt with by Lapworth (1956) with essentially the same conclusions. However, the statistics of correlation which were not given in that work are pertinent to ensuing discussions.

The method of analysis is that used by Hile (1937), Van Oosten (1942) and Carlander (1945). This approach involves the assumptions that fry plantings have relatively constant success (in terms of survival), that the year-classes make a large part of their total contribution at one age, and that this age remains the same over a long period of years. It must be assumed in addition that the levels of catch varied directly with abundance, since no early fishing effort data are available in the Lake Ontario case. It would thus happen that in an intensive fishery supported by plantings, a positive correlation should result when the numbers of fry planted each year are plotted against the catch values falling after the interval appropriate to the age of most fish in the catch.

The following correlation coefficients between the individual catch values and preceding levels of fry plantings were calculated from Tables I and II. The symbols used are as follows:

X' = the total annual whitefish catch in pounds $\times 10^4$
Y = number of fry planted in millions
r = coefficient of correlation
* = correlation at 5% level of significance, "significant"[5]
** = correlation at 1% level of significance, "highly significant"[5] and subscript n denotes the year in question.

Correlation between	r	*Degrees of freedom*
X'_n and Y_{n-3}	0.1592	18
X'_n and Y_{n-4}	0.3662	19
X'_n and Y_{n-5}	0.3377	18
X'_n and Y_{n-6}	0.5565*	17
X'_n and Y_{n-7}	0.3830	16
Y_n and X'_{n-1}	0.4517*	24

The correlation between plantings and the corresponding catch levels 6 years later is just outside the level (0.575) which is considered statistically highly significant for samples of this size. It has been shown in Fig. 6 and is illustrated in the strength of the last value above however, that the number of fry planted is at least in part determined by the number of whitefish available for the spawn-taking operations of the preceding fall. The latter in turn is related to the size of the commercial catch in that year. It is therefore important to know if the planting-catch correlation is a second order effect caused by a more basic stock-recruitment correlation.

The following series consists of serial correlations relating items within the catch series which are separated by various time intervals:

Correlation between	r	*Degrees of freedom*
X'_n and X'_{n-3}	0.7550**	19
X'_n and X'_{n-4}	0.7250**	19
X'_n and X'_{n-5}	0.6747**	19
X'_n and X'_{n-6}	0.5326*	19
X'_n and X'_{n-7}	0.2379	17

The effect of the strong downward trend in the catch data over the years following 1924 is reflected in the fact that the magnitudes of the above coefficients decrease with increasing time lags. When the individual catch values are compared with their next-following entries in column 3 of Table I, the coefficient is 0.9681** (35 degrees of freedom).

The values in the planting-catch series above all tend to have strong positive values also and the parallel trends in catches and plantings are considered responsible. This effect could mask any evidence of a stock-recruitment relation to be found in the catch data. To circumvent this difficulty, both variables were transformed to deviations from their respective trends.

[5]Application of these terms follows this usage in all cases.

In the catch series, a plot of catch in one year on catch in the year preceding is described by the line

$$\hat{X}'_{n+1} = 9.66 + 0.738X'_n \quad \ldots\ldots(1)$$

with the symbols as above. The theoretical X'_{n+1} values were calculated and the observed values subtracted from them. The resulting deviations appear in Table IX.

The deviations from the planting series were calculated in the same way. In the plot of Y_{n+1} on Y_n however, the scatter of the points was greater ($r = 0.4812$* with 24 d.f.) and the slope of the line biased somewhat downwards by one point in particular. The equation for the line is

$$\hat{Y}_{n+1} = 41.75 + 0.499Y_n \quad \ldots\ldots(2)$$

This line does not altogether eliminate the trend in the data, so the line was taken through the origin and the mean points, giving the slope 0.945, and the deviations were calculated as before. These values also appear in Table IX. For the correlations both variables were coded away from the negative.

As before, the data of Table IX were paired to compare the planting deviations in one year with the catch deviations occurring after various intervals. The coefficients of correlation were as follows using the same units and with the symbols as in the foregoing, but in the lower case:

Correlation between deviations	r	*Degrees of freedom*
x'_n and y_n	0.0938	35
x'_n and y_{n-1}	–0.0696	34
x'_n and y_{n-2}	–0.0107	33
x'_n and y_{n-3}	–0.1483	32
x'_n and y_{n-4}	0.1291	31
x'_n and y_{n-5}	–0.1977	30
x'_n and y_{n-6}	0.1482	29
y_n and x'_{n-1}	0.2779	28

No significant correlations appear within this series. The trends in the original data appear to have had some influence in the significant correlation found between fry plantings and catch six years later. It must be concluded, therefore, than an above- or below-average planting does not result in a significant corresponding departure from the trend in the subsequent commercial catch at any of the levels of separation tested. When the data were examined separately for the periods prior to 1944 and from 1944 to 1960, the results were essentially the same.

The serial correlations within the adjusted catch series were calculated and these are as follows for four of the intervals tested:

Correlation between deviations	r	*Degrees of freedom*
x'_n and x'_{n-4}	–0.01751	31
x'_n and x'_{n-5}	–0.02901	30
x'_n and x'_{n-6}	0.1132	29
x'_n and x'_{n-7}	–0.2168	28

The only positive correlation in this series is still not significant, but it may be observed that the value for the six-year separation has a positive tendency in this case as well as in that of the planting–catch deviation series.

The correlation between the planting deviations and the catch deviations reflecting the stock change was positive and fairly strong. The negative correlation values for the five- and seven-year intervals above indicate, however, that it cannot be held that the positive tendencies in the planting-catch deviation series were artifacts induced by the variations in stock levels in the years immediately preceding the plantings.

The low order of these correlations and their appearance at the four- and six-year separations are difficult to interpret either in terms of hatchery contribution or stock-recruitment effects. It seems most probable that they are incidental effects caused by the general alternation in the catch data.

This rhythm in the catches can be seen as an alternation in the data through all the years from 1925 to 1960. In the years 1925 to 1941, 7 out of 10 of the odd-numbered years had higher deviations from the catch trend than the even-numbered years adjacent to them. In the later years the rhythm was more often broken, but in even-numbered years it tended to be more pronounced. This has an important bearing on the results of the alternate-year planting experiment.

The evidence is quite convincing that the hatchery fry did not contribute enough fish to the fishery to alter appreciably the levels of the catches of most of the years studied. Beyond this, the limitations of the data prevent any evaluation of the actual contribution of the hatchery product. The contribution, if any, could be masked by either or both of the following. Firstly, the response of the catch to changing levels of abundance can be quite imprecise for several reasons, and a low regression might be obscured on this account. Secondly, nothing is known about the age composition of the catches of the early period, and any trend in modal age with the long-term decline in abundance is also a conceivable masking factor. The segregation of the data for the two time periods would not necessarily uncover such a bias.

CLIMATIC ASSOCIATION WITH VARIATIONS IN THE WHITEFISH CATCHES

The alternate-year rhythm in the whitefish catch statistics raised the possibility of an environmental effect, and an examination was made of the long-term air temperature records for the Belleville–Picton area. It was assumed that any controlling influence of temperature on brood strength occurs during the spawning or hatching periods, and that the air temperatures are reliable indicators of the condition in the water. The latter assumption has been validated by McCombie (1959), who was able to describe the seasonal relation between air and water temperatures by means of two linear regressions. The temperatures for November and April were studied, and in each case monthly averages were calculated from the daily means, and the values for either month subtracted from the respective long-term averages. The deviations thus derived for each month appear in Table X.

Various plottings indicated that the best correlation for the November series was that between the catch deviations (Table IX) and the corresponding November values five years earlier. The correlation coefficient is –0.3595, and this is significant at the 5% level. The April deviations were best correlated with the appropriate catch deviations falling four years later. The coefficient of correlation is 0.3358, and this is just outside the 5% level of significance. The multiple correlation coefficient (R) between the catch deviations and both the April and November temperature deviates is highly significant at 0.5225. This indicates that a total of 27% of the variation in the deviations from the catch trend is apparently accounted for in terms of the temperature conditions prevailing for the spawning and hatching of the year-classes produced four years earlier.

The adjacent November and following April air temperature deviations were next combined to produce single values for each year which are termed "thermal indices". This was done by substracting each November deviation algebraically from that of the April next following. The correlations above indicate that cooler Novembers and warmer Aprils are both associated with higher subsequent catches. The index relates the two such that a positive value occurs when a cooler-than-average November is followed by a warmer-than-average April, and a strong negative value indicates a warm November followed by a cold April. The index is designated by the year corresponding to that of the April value, so all indices are referable to the year-classes. These values also appear in Table X.

The use of the index incurred no significant loss of correlation. The correlation between these values and the catch deviates four years later is 0.5220, which is virtually the same as the multiple correlation coefficient and still significant at the 1% level. The deviations from the catch trend are shown in Fig. 8 plotted against their respective thermal indices four years preceding. The regression is not strong, but clearly very few of the catch deviations fall in either the upper left or lower right quadrants of the graph. The coefficients calculated for the various phasings between the indices and catch deviations are as follows, using the symbol x', for catch deviations as before, and z for the thermal index:

Correlation between	r	*Degrees of freedom*
x'_n and z_{n-2}	0.0619	33
x'_n and z_{n-3}	–0.2599	32
x'_n and z_{n-4}	0.5220**	31
x'_n and z_{n-5}	–0.1036	30
x'_n and z_{n-6}	–0.1082	29

The fry planting deviations and corresponding catch deviations four years following were reassessed in relation to the foregoing observations. The planting years with thermal indices greater than zero were segregated from those with zero and negative indices and the two plots of catch deviations against planting deviations four years earlier are seen in Fig. 9. Neither of the plots indicates correlation. It is noteworthy that most of the values for the years of negative

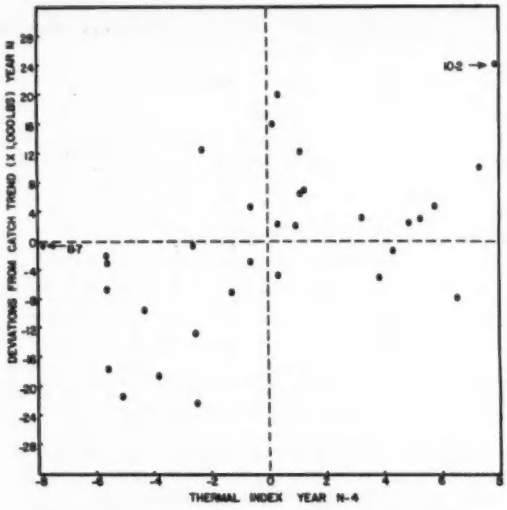

FIG. 8. The relation between thermal index and deviations from the whitefish catch trend, 4 years later.

index lie in the low ranges for both planting and catch deviations, with the reverse true of the data for planting years with positive thermal indices. This suggests that the weather accounted for most of the small correlation (0.1291) found between the fry plantings and catch deviates four years later. This is true in the case of the six-year separation also.

The cyclic tendency in the weather was such that climatic conditions four years apart tended to be in phase. The correlation between the thermal index in one year with that for the winter four years later is 0.4700, and this is highly significant. A five-year lag gives a strong negative correlation (–0.3716) however. This would mean that a strong year-class, as reflected by a positive catch deviation, entering the fishery at age IV more often than not faced unfavourable conditions for reproduction in the fifth winter. The generally lower plantings of these winters often followed positive catch deviations. This is illustrated in Fig. 10. The correlation between fry planting deviations and preceding-year catch deviations was also partitioned according to the thermal index levels for the intervening winters. The year n-1 catch deviations are used as the dependent variable in this case to facilitate comparison with Fig. 9. The scatter is great in both panels of the graph, but there is a negative trend to be seen for the years with negative indices and a positive trend for the years with positive indices. The points in the negative correlation (Panel A) are clustered slightly more closely around the intersection of the zero co-ordinates, suggesting that the positive correlation (0.2779) found for the combined data was largely created by the greater spread of the points in Panel B. The interpretation of these graphs appears to be that for winters of negative thermal index (and thus generally

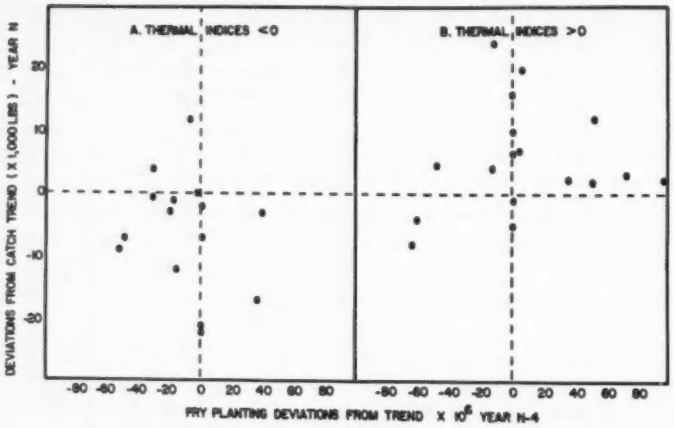

FIG. 9. The relation between fry plantings and catch deviations 4 years later when (A.) thermal index in the hatching year is negative and when (B.) thermal index is positive.

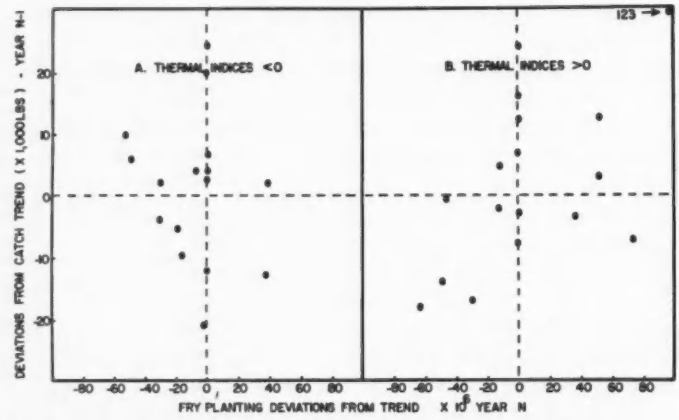

FIG. 10. Fry plantings and catch deviations in the years preceding at 2 thermal index levels.

warmer Novembers) the spawn-takes and resulting plantings were small regardless of preceding stock levels. In the favourable winters large stocks produced large plantings. It must be concluded, therefore, that the variations in the number of fry planted were determined by the stock levels in the long term, and controlled partially by the weather from year to year.

When the serial correlations for the catch deviation series were calculated separately for the years with positive and negative thermal indices, the results were similar to those discussed above. No significant correlations were found,

and the one positive tendency (in the combination x'_n and x'_{n-6}) which had been noted, was obliterated. The weather-catch deviation correlation suggested that the whitefish enter the commercial catch at age IV. If there is a stock effect and first spawning is at age IV, the pulses of catch should therefore be separated by five years. This is not the case and the only evidence is that the catch pulses created by the entry of larger year-classes are often immediately preceded by good winters for reproduction.

The conclusion reached from the foregoing is that the dominant factor involved in the rhythmic catch fluctuations is climatic. The weather influenced the size of the fry plantings, but there is no indication in these data that the fry plantings influenced subsequent catch levels. The strength of the weather-catch correlation is such that it must also be judged that changes in the age composition sufficiently great to mask such a correlation are not likely to have occurred.

The weather data offer a possible explanation of the decline in abundance from the 1920 peak. The conditions for reproduction were good in a number of years between 1915 and 1922. There then followed a series of poor years until 1933, when more or less normal fluctuations were restored. The thermal indices for the years 1915 to 1922 averaged 1.5 units above average, while those for the period 1923 to 1932 averaged 2.4 units below average. One would surmise that low levels of fishing intensity coupled with good conditions for reproduction permitted the accumulation of a number of large year-classes early in the 1920 decade. Heavy fishing ensued and the poor year-classes probably produced in the 1924–1933 period permitted the harvest rate to exceed the recruitment — a condition which persisted through the 1930 decade.

This suggested role of stock density cannot be verified with these data. It is possible that these measures of stock and recruitment are too crude to show the (probably) low order relationship in the presence of the strong temperature-catch correlation. However, the temperature data exhibited no long-term trend over the years studied, and several recent periods have been as favourable climatically as the 1915–1922 period. That none of these caused a return to a high abundance level can only be attributed to the reduced stock density levels or to some unknown environmental change(s).

RECRUITMENT AND THE ALTERNATE-YEAR PLANTING EXPERIMENT

The most striking feature of the estimates of year-class strength in Table VII is their alternation in strength. Only the three year-classes of 1951, 1955 and 1957 of the twenty produced between 1938 and 1957, proved stronger than those of the adjacent, even-numbered years. Since the alternation in strengths of the year-classes appeared as early as 1938, it was not likely established by the alternation in the hatchery operations.

The variations in the estimates of year-class strength were studied by means of correlation analysis, as before. The actual values for fry plantings were used in this case.

The following symbols were used for the examination of the fry planting effects:

X = minimum year-class strength
Y = number of fry planted
z = thermal index

and subscript n denotes the year in question.

The following are the coefficients calculated:

Correlation between	r	*Degrees of freedom*
X_n and Y_n	0.3597	19
X_n and z_n	0.4405*	19
Y_n and z_n	0.03147	19

In this case, the correlation between the thermal indices and year-class strength is somewhat lower than that involving the catch data, but still significant. The correlation between recruitment and the fry plantings is fairly high. This difference from the analysis of the catch data may have resulted from the removal of the trends from the statistics in that case, and the new value suggests that the plantings may have played a more important role.

The multiple correlation coefficient (R) for the relation between year-class strength and the two variables, fry planting and thermal index, is 0.4853*, indicating that about 24% of the variability in year-class strength is thus accounted for.

As in the last section the year-classes were segregated according to whether the thermal indices involved were positive or negative. The solid points in Fig. 11 are the estimates of year-class strength plotted on fry plantings for the years with negative indices. The open circles denoting year-classes produced in favourable years are uncorrelated with the fry planting level; several of the largest year-classes were produced in years of low or non-planting.

The correlation for the negative years is 0.7022 (d.f. = 19), which is statistically highly significant. The equation of the line describing these points is:

$$X = 44.42 + 1.287\ Y \qquad \ldots\ldots(3)$$

There is no indication of a temperature dependence in these data, and any error in the estimates of year-class strength (which would act to make the estimates for earlier year-classes relatively too low) could only act to reduce the effect because of the reduction in planting levels in recent years. It therefore seems tenable that in years of unfavourable conditions for reproduction the effects of the fry plantings were more distinct. If the stock effect is considered constant, regression indicates a hatchery contribution of 1300 fish per million fry planted.

The intercept of the line suggests that an average of 44,000 recruits resulted from the four years which were unfavourable for reproduction and not supported by fry plantings. It is known, however, that the stock levels were much higher in the early years, when plantings were also much higher. This may mean that the foregoing regression is at least in part dependent on the higher stock levels. The next section will assess this relationship by examining the effects of fry plantings on parent–progeny ratios.

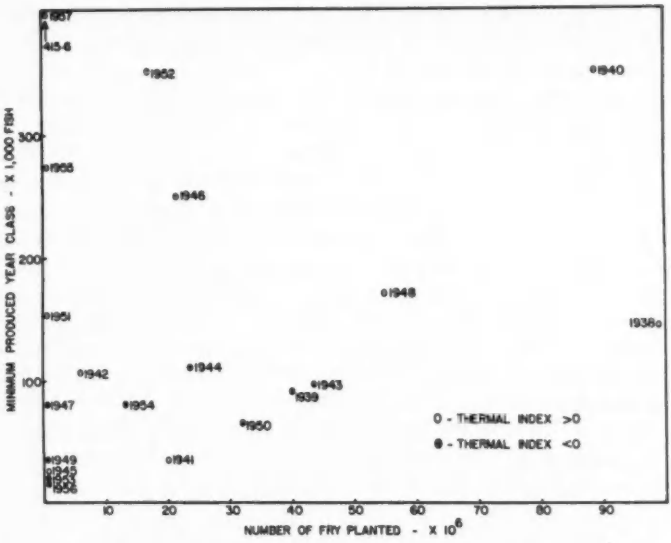

FIG. 11. The relation between fry plantings and minimum estimates of the strengths of the corresponding year-classes.

STOCK DENSITY AND RECRUITMENT

Minimum estimates of population size have been prepared in the manner of Fry (1949). In this approach, the virtual populations of all the various year-classes present together before the start of fishing in any year are summed. For example, (see Table VI) at the beginning of 1944 there were at least 43,190 age III fish of the 1941 hatch, at least 347,878 age IV fish, and so on, reading diagonally upwards to the right in the table. The total for this series is 532,788 fish, and this is an estimate of the numbers of fish age II and older at the end of the previous fishing year. When the sums making up this total are corrected by the appropriate sexually mature fractions of the various age groups, the total can be taken as a minimal estimate of spawning stock density. In this case it must be assumed that these estimates are in constant proportion to the average stock size during the spawning period because of the large catches often made at this time.

Since 1944 is the first year for which a summation of virtual populations is possible, no estimates of spawning stock density are available to compare with the 1938 to 1943 year-classes. The total virtual populations for fish age IV and older (age III and older in the preceding fall) appear in Table XII.

Table XI summarizes the observations made during the Hay Bay spawning runs of 1953 through 1958. In all years except 1953, virtually all whitefish captured were tagged and released after examination, so it is not likely that the sex ratios were biased by selection within a catch or repeated captures of the

same fish. Considerable variation in sex ratio was noted from day to day within the individual runs, but in general the males tended to predominate both early and late in the spawning seasons.

The sex was determined by pressing the abdomen of the fish to extrude ova or milt. Sex identification was more positive for the males because milt was usually detectable from the earliest appearance of the fish in October until the freeze-up. The grand total for each year exceeds the sum of the males and females by a small number in all years, and the unsexed fish constituting the difference were usually "green" females whose ova had not yet been released into the body cavity. The first year of the series was exceptional in that sex observations were not made in all cases. That this fraction for the other five years was very small (2.4%) is taken as evidence that only sexually mature individuals were captured. Fish were randomly selected for tagging in 1953, and fish which had been retained by the spawn-takers for ripening were avoided when they could be recognized, so it is felt that these data are not seriously biased.

It seems quite probable that these observations were representative of the Hay Bay spawning populations because the trapnets used have always had sufficiently small meshes to retain all whitefish down to the one-year-old size range. The representativeness of the Hay Bay observations in relation to all the spawning stocks must be assumed, but the considerable similarity between the commercial catch sampling data and the Hay Bay data with respect to the relative strengths of the various year-classes makes it quite likely that this is so.

The totals for all males at each age are shown at the bottom of Table XI, and they are also expressed as percentages of their respective totals. The female percentages corresponding are taken as the remainders from the male values It can be seen that relatively few age II fish are captured and these are nearly all males. Females average 23.3% of the age III fish, and the percentage increases steadily with increasing age. The females are numerically slightly more abundant than males at age V and they predominate at higher ages. This effect has been reported by Van Oosten and Hile (1949), Hart (1930) and other workers and appears to indicate a mortality rate differential between the sexes with increasing age.

In the absence of sex ratio data for the stocks at large, it must be assumed that all fish older than age V are mature and that males and females are equally represented in the population at ages III and IV. If it is taken then that all the males are mature at age III and spawn each fall thereafter, it can be estimated that sexually mature females constitute $\frac{270}{1190} \times 0.5$ or 11.3% of the age III population. Similarly it would be inferred that at age IV $\frac{248}{528} \times 0.5$ or 23.5% of the stock is made up of mature females. The values 56.2, 60.2 and 73.5% at the bottom of Table XI are taken as the mature female fractions in the older groups.

The age III and age IV fish are always less abundant on the spawning grounds than in the (virtual) population in general, and this cannot entirely be explained on the basis of the absence of the immature females. Comparable population estimates and spawning stock data are available for the falls of 1953 through

1956 and these are summed in the following to demonstrate the age composition differences. Age VII and all greater ages are combined to avoid the smaller samples.

		Age				
1953–1956		III	IV	V	VI	VII +
Total Virt. Pop.	No.	475,448	178,405	34,659	10,767	8,075
	%	67.2	25.3	4.9	1.5	1.1
Total Spawning Fish	No.	1332	805	325	113	65
	%	50.4	30.5	12.3	4.3	2.5
Spawning Males		1023	509	138	43	17
Spawning Females		234	245	119	56	35

There are some differences between ages, but the virtual population curves for the various years are similar to the corresponding spawning run curves through the three age groups V, VI and VII+. For example, in the above totals the average slopes for the virtual and spawning run data are calculated as:

$$\frac{8075 + 10{,}767}{10{,}767 + 34{,}559} = 0.41 = \frac{65 + 113}{113 + 325}$$

On the basis that the average mortality rates are the same it can be inferred that the sex ratio in the virtual and spawning populations are similar. Males made up 48.5% of the sexed spawning fish age V and older and the males in the virtual populations of these ages are calculated as:

$$0.485\ (34{,}659 + 10{,}767 + 8075) = 25{,}964.$$

The ratio of age V-and-older males to age III males in the spawning run catches is $\frac{198}{1023} = 0.194$. For an hypothesis that one-half the age III virtual population consists of mature males, the comparable ratio is: $\frac{25{,}464}{0.5 \times 475{,}448} = 0.109$. This suggests that there were almost twice as many age III males extant as appeared in the spawning run catches. An estimate of the age III fraction is calculated in the relation:

$$ {}_{m}k_{III} = \frac{{}_{m}V_{V+} \bullet {}_{m}C_{III}}{{}_{m}V_{III} \bullet {}_{m}C_{V+}} = 0.281 \qquad \ldots\ldots(4)$$

where k = fraction mature
V = virtual population
C = spawning run catch

and subscript m denotes males and roman numerals indicate age. The fraction maturing is similarly calculated for age IV, as 0.374. It is therefore estimated that 28% of the age III fish and 37% of the age IV fish are mature males.

The new estimates of the female fraction of the virtual population maturing at ages III and IV are now calculated from the sex ratios at the bottom of Table XI as $0.281 \times \frac{270}{1190} = 0.064$, and $0.374 \times \frac{248}{528} = 0.176$.

The foregoing analysis indicates that 56% of the males mature at age III and 75% mature at age IV. Similarly 12% of the females mature at age III and 35% at age IV. This statement requires that the sex ratios in the age III and age IV populations approach unity. Further data will be required to test this, but this does not bear on the mature fractions of the totals as calculated. The data do not, however, take into account changes in the sex ratios or the age of first maturity which may occur from year to year. The virtual populations are also a source of error since their relations to the true populations probably vary with age. Since the virtual populations are always smaller than the true populations, however, and since the mesh selection was always at a minimum in the spawning run catches, it is felt that the maturity corrections are conservative.

Estimates of the numbers of mature female fish for each year of the 1943–1956 series are presented in Table XII. These are summed from the entries in Table IV (ages IV+) when corrected by the female maturity fractions given above and used in the expression:

$$ {}_fV_{\text{spawning}} = \Sigma\ ({}_fk_j \bullet V_j) \qquad \ldots\ldots(5) $$

where the subscripts, f, denotes female and j, the jth age.

Also given in Table XII are the totals for the virtual populations of age V and older. It is noteworthy that the two columns of figures are quite close in average, and vary in parallel fashion. This reflects the heavy dependence of the spawning population on the older fish.

The relatively small contribution of the four-year-old fish to the spawning stock offers a possible alternative interpretation of Fig. 10. The positive catch deviations are taken to reflect the entry of stronger-than-average year-classes into the fishery at age IV. The spawning run observations suggest that the greatest impact of these year-classes on the spawning stock would not be felt until the following year (and this of course would not be detectable in the catch data). The sixth winters (following age V, of the year-class) were more often than not favourable for reproduction, and *also* the years of spawning stock increase, and resulting larger spring planting. It would happen, in this circumstance, that a year-class creating a pulse of catch at age IV, and spawning successfully at age V, would be responsible for a following year-class creating a catch pulse six years after the first. This rhythm, superimposed upon that established by the annual temperature variations, would provide a more complete explanation for the predominantly alternate-year variation in the catch data.

The spawning potential of the various virtual populations has been estimated by taking into account the increasing fecundity of the females with advancing age. The following are the length averages for the female whitefish of Table XI:

Female	III	IV	V	VI	VII +
Average fork length (inches)	15.6	16.4	16.7	16.6	18.3
Average weight (lb)	1.85	2.20	2.35	2.30	3.18

These size values follow a line similar to that seen in Fig. 2 but in this case it is felt that the upward bias in the early ages is due to the fact that only the larger fish mature and the effect is similar to that induced by mesh selection.

The average weight values in the second row were calculated from an equation which has been derived from the commercial catch sampling data:

$$\log \hat{W} = 3.426 \log L - 3.816 \qquad \ldots\ldots(6)$$

where

W = weight in pounds
L = fork length in inches.

The total weight of female spawners was calculated by applying these averages to the virtual populations in the expression:

$$_fW_{\text{spawning}} = \Sigma\ (_fk_j \bullet \overline{_fW_j} \bullet V_j) \qquad \ldots\ldots(7)$$

with the symbols as in the foregoing.

The various totals appear in column 4 of Table XII.

In a series of 29 gravid female whitefish (whose ovaries were still intact), the fecundity averaged 9886 ± 1650 eggs per pound of fish. This value is similar to those reported by other investigators (cf. Hart, 1930), and for convenience in computation it was rounded to 10,000 eggs per pound. The weight values of column 4 were all multiplied by this value, and the resulting products are seen in column 5 of Table XII as minimal estimates of spawn potential expressed as millions of eggs.

The spawn potential estimates are seen plotted in Fig. 12 against the corresponding estimates of year-class strength (Table VII). As in Fig. 11, the solid

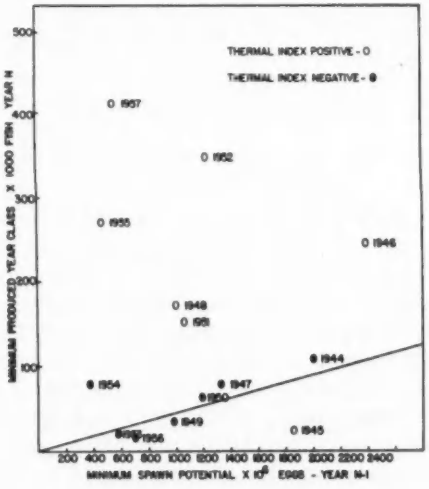

FIG. 12. Minimum estimates of year-class strength and the corresponding estimates of spawn potential for the falls preceding.

circles represent the years of negative thermal index, and the open circles those with positive indices. The two years 1945 and 1954 are somewhat aberrant but the rest of the points present an interesting configuration.

The year-classes produced in the unfavourable years (except 1954) rise along a line which (disregarding minor irregularities) has a slope value close to 1.0. The average ratio for the six years-classes is 44 recruits per one million eggs potential. The grand average weight for the females of Table XI is 2.2 lb (estimated from equation 6), and this indicates an average fecundity of 22,000 eggs per fish. It is therefore estimated that one million eggs would represent the spawn of about 45 fish. The construction line in Fig. 12 was given the slope value of 45 fish per million eggs potential. The recruits are not all females and many of the recruits do not succeed in spawning, so this line must represent less than one-half of stock replacement. This finding differs from that of Shepard and Withler (1958), who showed that the least successful year-classes of Skeena River sockeye salmon (*Oncorhynchus nerka* (Walbaum)) were usually at least as large as the total spawning stocks which produced them. In that case each brood had only one opportunity to reproduce itself, and it is reasonable that the minimum reproduction rate would be lower for multiple spawners like the whitefish. The recruitment estimates are slightly reduced by the exclusion of the older fish, but in general the two sorts of virtual population estimates are affected by similar error. Particularly since most of the year classes under consideration were fished since 1950, it seems unlikely that the above observation is seriously influenced by errors of estimation.

The year-classes of the favourable winters averaged eight times larger than those produced in the unfavourable years, and several quite large year-classes resulted from meagre spawnings. It is recognized that the number of year-classes involved in Fig. 12 is too small to permit close interpretation, but the overall similarity between this graph and the Type C reproduction curve (Ricker, 1958) presented by Shepard and Withler (1958) is noteworthy. In this case maximum recruitment occurred at a lower stock level, but in common with the salmon study the range of variation in whitefish year-class strength appears to have been much narrower in the earlier period of higher stock density.

The reasons for the departures of the 1945 and 1954 year-classes from the pattern are not clear. Two points should be borne in mind, however. Firstly the analysis assumes a constant relationship between the number of whitefish hatching, and those surviving to enter the fishery. The strong correlation between the weather and subsequent catches in this fishery suggests that this may be generally the case, but the possibility of occasional catastrophic loss, or severe reduction in the numbers of a year-class at any time during the life history, must not be overlooked. In view of the substantial residual variance in the temperature–year-class strength relationship, the possibility of an occasional strong year-class produced in apparently less than ideal environmental conditions is also not remote. Interpretation of deviations from alignment in the six negative-year points other than 1954 in Fig. 12 should also be approached with caution for the same reasons.

The question of stock replacement was explored further by relating individual year-classes to the total progeny for which they were responsible. For the estimates of the progeny, the individual values for total mature female weight in equation (7) were calculated for each age in each spawning year, and converted to estimates of spawn potential. These, expressed as fractions of the total estimated for any spawning, are applied to the estimates of the produced year-classes to obtain estimates of the numbers of fish contributed by each spawning year-class. These values are shown in Table XIII. The total progeny of any year-class can now be summed by following the successive spawnings diagonally downwards to the right in the table. For example, the minimum size of the 1940 year-class was 351,370 fish. At age III its contribution to the 1944 year-class is given in Table XIII as 22,353 fish. For the next year it is estimated to have contributed 12,508 fish of the 25,578 fish harvested. The last value for the year-class is the 53,530 fish of the 1948 year-class. As before, this represents all fish age VII and older, but the value can be taken as largely age VII fish. The total progeny produced by the 1940 year-class is estimated as 311,257 fish. Only the ten year-classes 1940 through 1949 can be included in this series, since the 1957 year-class is the last for which an estimate is available. The estimates for the year-classes and their progeny are listed in Table XIV.

These estimates are subject to the limitations discussed earlier in connection with the use of virtual populations, and in addition they are, for comparative purposes, even less independent. The significant feature of Table XIV, however, is the high correlation between the two series (0.9233) in the face of the pronounced climatic effect. The new parent: progeny ratios average to 1.05. A trend is evident in the range of the ratios of Table XIV through the series, and it is likely that the progeny from the more recent year-classes would have shown still greater scatter about the replacement level. The increasing reliance of the stock on one spawning diminished the probability of smoothing out the influence of the climate over several spawnings, and the stock apparently compensated by producing more progeny per parent in the favourable climatic years at the lower population levels.

The general decline in the sizes of year-classes produced in negative index years through this series, coincident with a reduction in stock levels, fortifies the suspicion that the negative-year correlation of Fig. 11 was an artifact created by the association of the larger plantings of the earlier years with higher stock levels. By conversion, in fact, it appears that the average for the values of Fig. 12 — 44 recruits per million eggs potential — is a higher slope value than that for the regression of year-class strength on fry plantings — 1300 recruits per million fry planted. Table XII shows that the average spawn potential for the spawnings from which plantings were made was 1358 millions of eggs. The corresponding average planting was 27 millions of fry — one-fiftieth of the presumed natural reproduction. The value corresponding to 1300 is therefore $50 \times 44 = 2200$ recruits. The two data series are not strictly comparable since the Fig. 12 series involves fewer years, but it seems likely that any significant contribution of the fry plantings would have resulted in a substantially higher slope value.

It is noteworthy also that if the 1954 datum is disregarded, the stock-recruitment correlation is much the stronger statistical relationship. This would be expected if the planting-recruitment correlation were a secondary effect based on the relation between the stock level in any spawning and the resulting fry planting.

Table XV lists the recruit: spawn potential ratios for the various year-classes. For the favourable years it will be seen that the average for the unsupported year-classes was actually higher than for the year-classes which were supported by hatchery fry, so there is little question that the hatchery fish were far outnumbered by their wild counterparts in these years. It will also be observed in this Table that there were only three year-classes produced in negative-index years which were also supported by plantings. Two of these, the year-classes of 1944 and 1950, have lower values than that for the unsupported year-class of 1947. The other supported year-class, that of 1954, received the lowest fry planting (13 millions) of the series, and yet produced more fish than the 1950 year-class which was supported by a planting nearly three times larger. In the opinion of the author it is doubtful that this year-class gained its strength through the addition of hatchery fry.

The study as a whole appears to offer two alternative propositions. The first of these is that fry plantings bolstered the fishery at the rate of approximately 1300 recruits per million, at least in years when the weather did not favour natural reproduction. This requires that the suggested stock-recruitment effect be rejected. The concurrent declines in stock and recruitment (in unfavourable years) are therefore considered unrelated while the similarly concurrent declines in the plantings and recruitment are considered causal. The second proposition is believed to be more firmly supported by the data and it is offered as a conclusion for this work, as follows. Whatever the numerical contributions of the hatchery fry to this fishery, in most years their levels must have been beyond the limits of detection in the data at hand, and certainly below any level of economic significance to the fishery.

DISCUSSION

The findings of this study with respect to the effects of fry planting are in agreement with those of a number of previous investigators. Hile (1937) was unable to relate fry plantings to subsequent abundance in the yellow pickerel fisheries of Lakes Huron and Michigan. Van Oosten (1942) similarly found no such relation in the whitefish fishery of Lake Erie. Carlander (1945) found no correlation between year-class strength and hatchery support in the yellow pickerel fishery of Lake of the Woods, Minnesota. Miller (1946) studied the effects of alternate-year whitefish plantings in a number of Alberta lakes, and could find no evidence of hatchery contribution to the reproduction. It is noteworthy that Miller found that the strengths of the year-classes in any year tended to be in phase over all the lakes, suggesting a common climatic influence.

An implicit assumption in artificial propagation used for fishery maintenance is that the mortalities encountered during the incubation of the eggs and the

rearing of fish in a hatchery are sufficiently small, when compared to natural losses at the same stages, to compensate substantially for the great initial numerical disparity between the eggs spawned naturally and those taken for the hatchery. The apparent importance of spring temperatures in the determination of year-class strength, as indicated in the present study suggests that losses after hatching are important, and these must affect the stocked fry as well as the wild. The hatchery advantage would be further reduced if the fall temperature effect suggested here influenced the spawn-take or the survival of the eggs in the hatchery also.

It has been suggested (Miller, 1946· Dymond, 1956) that hatchery fry make no detectable contribution because the environment imposes absolute limits on the survival, and reproduction provides fish well in excess of the limits in most years. The surplus, whether of wild or hatchery origin, therefore must die. The relationship between stock density and recruitment suggested in the interpretation of Fig. 12, however, offers an alternative explanation. At higher stock levels in the most favourable environmental circumstances it is tenable that the reproduction exceeds the limits of the environment, and at such times mortality becomes related to density. In the unfavourable years on the other hand, these data suggest that mortality may have acted to reduce the year-classes by some roughly constant proportion regardless of the absolute numbers of progeny involved. This is applicable to the range of stock levels seen, but presumably above some upper limit mortality in this case would also become density-dependent. This raises the possibility that the year classes of unfavourable climatic years might be bolstered by large fry plantings.

In contrast to the studies referred to above, the fisheries of two large Swiss lakes have been reported (P. Laurent, Directeur de la Station de Recherches Lacustres, Haute-Savoie, France, personal communication) completely dependent on coregonid fry plantings. These are the lac de Zürich and the lac de Bienne, both of which are without natural whitefish reproduction. In the former, fry survival is reported at 0.4%, and in the latter lake it ranges between 0.2 and 0.4%. Both lakes are heavily planted. In Bienne the annual plantings average 8000 fry per hectare (3238 fry per acre). This is a much more intensive program than most of those reported in North America. For example, the largest fry planting made in the six lakes studied by Miller (1952) was 521 fry per acre, and the average fell well below this. In Lake Ontario, if the Bay of Quinte and the waters of the eastern basin (ca. 850 sq mi) are considered the full range of effect of the fry plantings, the largest planting ever made involved only 380 fry per acre. The average for the 1940–1954 period amounted to only 50 fry per acre.

Only one North American report indicating a positive effect of fry planting on year-class production has been located. This concerned the alternate-year yellow pickerel planting study conducted by Carlander *et al.* (1960) in Clear Lake, Iowa, and in that case it was suggested that the success of the plantings may have been related to the planting intensity, which ranged between 5449 and 9566 fry per acre. It is likely that such intensive plantings are only feasible in small lakes. A test of various fry planting intensities, however, might be expected to yield useful information on fry mortality.

The mechanisms underlying the suggested temperature effect on year-class production are unknown. Whitefish have been observed in spawning condition at water temperatures ranging from 48° down to 40°F., and possibly fast cooling in the fall encourages the occurrence of peak concentrations of fish at some optimum temperature. Another possibility is that early ice cover provides protection from wind-induced damage to the deposited spawn. Miller (1952) was unable to demonstrate such a relation in the Alberta whitefish lakes he studied, but the degree of the effect could vary with conditions of wind exposure and spawning depth. There is the possibility also of a direct temperature effect on the survival of the newly fertilized eggs. Hart (1930) discussed the influence of fall temperatures on the length of the whitefish incubation period, and suggested that since winter and spring temperatures were similar for Lake Nipigon and the Bay of Quinte the five-week longer incubation observed in the former area must be due to the cooler temperatures in the period immediately following the deposition of the eggs. The variation in median hatching date from year to year has not been studied but it is likely dependent on the temperatures in the early developmental phases, at least to some degree.

As Hart (1930) suggested, the availability of (Entomostracan) food for the young whitefish could be a critical factor in the spring, and the timing of the growth of the populations of these organisms is related to spring temperatures. The evident lack of influence of degrees of "favourableness" or "unfavourableness" in relation to reproductive success indicates that within the narrow range of temperatures observed other factors are relatively important. It may also suggest that the whitefish are adapted to the temperature means and any appreciable deviation from them can have a pronounced effect. For example, if the coincidence of the spring plankton pulse with the whitefish hatch is a critical requirement for a strong year-class, an average temperature only slightly below the long-term average in April could mean a delay of days between the completion of yolk sac absorption (the timing of which is at least partly predetermined) and the appearance of readily available food. Observation in the hatchery has indicated that the first feeding must come within a few days after the depletion of the yolk, or the chances for survival are impaired greatly. It would seem plausible that, in the event of a delay, only a certain fraction of the larvae would be strong enough or adapt quickly enough to a different food supply to survive. The speculative nature of the foregoing should be emphasized. The temperature effect suggested by these data is an interesting one, and it was useful as the only available means of reducing the year-class strength variance for the analyses. It cannot be validated, however, until further research has explored the nature of its operation.

The interrelations among the variates considered in this work have emphasized the limitations of experiments involving alternate hatchery closure. The difficulties arising out of the phasing of the planting years with years of successful natural reproduction, for example, might have been avoided if the planting years had been randomized within the study period. The relation between numbers of fry planted and the contemporary stock levels also introduced

a complication, and this could have been avoided by importing hatchery fry from elsewhere to maintain a consistent planting intensity. As mentioned above, however, future experiments of this sort might be profitably arranged to test the effects of a broad range of planting levels as well.

That the average catch of whitefish was not increased with more intensive fishing in recent years has been attributed earlier in this paper to a relatively low rate of natural mortality in the fished part of this stock. There is the alternative possibility that an increase in natural mortality occurred along with the increase in fishing mortality, but this seems rather less likely. The sea lamprey (*Petromyzon marinus* Linnaeus) is the only known predator on the adult whitefish, and wounds and scars are commonly seen on fish which have survived attacks. The commercial fishermen recall that the lampreys were very abundant in the 1920 decade but have noticed no striking recent changes in their abundance. The whitefish is the most important forage of the lamprey during the summer months, and it is interesting to compare this evidently light predation with the recent destruction of the upper Great Lakes lake trout stocks after the invasion of the sea lamprey.

The implications of the suggested relationship between stock levels and recruitment are very significant in relation to the management of this fishery. It has been shown that the increased fishing pressure of the recent years did not produce more fish, but rather about the same number of smaller fish with an increased year-to-year variation. This was partly due to the increasing confinement of the catch to one age, and partly to the increased variability in recent years in year-class strength. The most reasonable explanation of the fact that both the largest and the smallest year-classes of the series occurred in the recent period appears to be that more young fish produced in the favourable years were able to survive at the reduced stock levels. It is possible that the age of first maturity declined along with the reduction in the abundance of older fish, but the compensating changes in rate of growth which might have been expected to accompany such changes were not in evidence, and there is little doubt that the decline in abundance has been accompanied by a decline in the size of the spawning population.

The range of variability in year-class strength was about twenty-fold. This is close to Ricker's (1958) level "B" of environmental effect on recruitment, but the effect in this case is substantially reduced over several spawnings. This "smoothing-out" effect of multiple spawnings was illustrated in Table XIV. Assessment of the characteristics of the reproduction curve, or curves, was not possible because the virtual populations were used in both parent and progeny estimates, introducing an autocorrelation. In addition, the steady decline of the stock through the years studied prevents obtaining an estimate of sustainable yield at any one stock level. It might be said that some of the capital was taken as well as all the interest in each year, obscuring the true rate of interest.

It can be argued alternatively that the decline in the stock occurred as a result of some progressive deterioration in the suitability of the waters as whitefish habitat. Increases in the human population and in the level of

industrialization during the past twenty years make it almost a certainty that there have been some important changes in at least the Bay of Quinte waters. It is possible that such things as increasing turbidity and siltation have acted to limit spawning facilities and/or reduce the survival of the deposited eggs, while the probable general enrichment of the water (say) encouraged survival of the fry through an improved invertebrate food supply in the favourable climatic years. Similarly there have been numerous changes in other fish species populations, many of which could have influenced the whitefish abundance. It is the author's opinion, however, that in this case, the fishery-induced changes have been of primary importance with the other influences playing lesser roles. An important basis for this contention is the fact that there were no differential changes apparent in the fall catch data, for the recent years (1948–59), which would have indicated that the size of the annual Bay of Quinte spawning run varied other than in roughly parallel fashion with the runs to the Lake Ontario shoals, where the water is clearer (and presumably cleaner) than that of the Bay of Quinte. The most important of these spawning grounds lies along the south shore of Prince Edward County westward from Point Traverse to Salmon Point, and this area is also without the large littoral communities of fish which are found in the Bay. This is not conclusive evidence by any means and in the absence of information on environmental influences on reproductive success, the present hypothesis can only be tested by assessing the degree of reversibility of the observed changes.

It is felt that this stock must be considered seriously overfished. The result of the current trend must almost certainly be the economic collapse of the fishery. The fishery has only survived the effects of the poorer year-classes through the slightly higher prices paid for whitefish in the off-years, and this has encouraged the operators to fish at increasingly higher intensities. It is felt that only the climatic rhythm and the larger recent favourable-year hatches have sustained the fishery in the face of the continued stock decline. At some level of stock between that which produced the 1957 year-class and zero, it seems reasonable that the numbers of spawners will begin to limit the sizes of the year-classes, regardless of conditions for survival. In addition any interruption in the rhythm resulting in the failure of two or more years-classes could be expected to have a drastic effect. It is felt, on the other hand, that there are still grounds for optimism concerning the future of the whitefish in Lake Ontario and management should proceed at once on this basis, with measures to determine the extent to which the stock can be restored to its former levels.

CONCLUSIONS

1. The long-term catch trends in the whitefish fishery were paralleled by the sizes of the annual plantings of fry which evidently exerted no control on the trends.
2. Temperatures at spawning and hatching appeared to have an important influence on subsequent production.
3. The phasing of the weather conditions during the alternate-year hatchery closure experiment was such that large spawning stocks, heavy fry plantings and favourable climatic conditions all tended to coincide.

4. In the alternate-year planting experiment, the effects of the plantings were not discernible.
5. An effect of the size of spawning population on subsequent recruitment is suggested for years with unfavourable conditions for reproduction. The generally downward trend in stock is attributed to overfishing.

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The original manuscript was reviewed by Professor Fry and Professor J. R. Dymond. Dr W. E. Ricker read the final draft. The comments and suggestions of these gentlemen were very helpful and are gratefully acknowledged.

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REFERENCES

BAKER, M. H., AND H. H. BROHM. 1960. A modified roller press for scale impressions. *Canadian Fish Culturist*, No. 26, pp. 31–34.

BISHOP, YVONNE M. 1959. Errors in estimates of mortality obtained from virtual populations. *J. Fish. Res. Bd. Canada*, **16**: 73–90.

CARLANDER, KENNETH D. 1945. Age, growth, sexual maturity and population fluctuations of the yellow pike-perch *Stizostedion vitreum vitreum* (Mitchill) with reference to the commercial fisheries, Lake of the Woods, Minnesota. *Trans. Am. Fish. Soc.*, **73**: 90–107.

CARLANDER, K. D., R. R. WHITNEY, E. B. SPARKER AND K. MADDEN. 1960. Evaluation of walleye fry stocking in Clear Lake, Iowa, by alternate-year planting. *Ibid.*, **89**(3): 249–254.

DYMOND, J. R. 1928. Some factors affecting the production of lake trout (*Cristivomer namaycush*) in Lake Ontario. *Univ. Toronto Stud., Biol. Ser.*, No. 31, pp. 29–41.

1956. Artificial propagation in the management of the Great Lakes fisheries. *Trans. Am. Fish. Soc.*, **86**: 384–392.

DYMOND, J. R., J. L. HART AND A. L. PRITCHARD. 1929. The fishes of the Canadian waters of Lake Ontario. *Univ. Toronto Stud., Biol. Ser.*, No. 33, pp. 1–35.

FRY, F. E. J. 1949. Statistics of a lake trout fishery. *Biometrics*, **5**(1): 27–67.

HART, J. L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis* (Mitchill) in the Bay of Quinte, Ontario. *Contrib. Canadian Biol. Fish. New Ser.*, **6**: 165–214.

HILE, RALPH. 1937. The increase in the abundance of the yellow pike-perch, *Stizostedion vitreum* (Mitchill) in Lakes Huron and Michigan, in relation to the artificial propagation of the species. *Trans. Am. Fish. Soc.*, **66**: 143–159.

1941. Age and growth of the rock bass *Ambloplites rupestris* (Rafinesque) in Nebish Lake, Wisconsin. *Trans. Wisconsin Acad. Sci.*, **33**: 189–337.

KOELZ, WALTER. 1926. Fishing industry of the Great Lakes. *Rept. U.S. Dept. Comm.* for 1925, Appendix XI, U.S. Bur. Fish. Doc. 1001, pp. 554–617.

LAPWORTH, E. D. 1956. The effect of fry plantings on whitefish production in Eastern Lake Ontario. *J. Fish. Res. Bd. Canada*, **13**: 547–558.

MCCOMBIE, A. M. 1955. Some relations between air temperatures and the surface water temperatures of lakes. *Limnol. Oceanogr.*, Vol. **4**, pp. 252–258.

MCCOMBIE, A. M., AND F. E. J. FRY. 1960. Selectivity of gill-nets for lake whitefish *Coregonus clupeaformis*. *Trans. Am. Fish. Soc.*, **89**: 176–184.

MILLER, R. B. 1946. Effectiveness of a whitefish hatchery. *J. Wildlife Management*, **10**: 316–322.

1952. The relative strength of whitefish year classes as affected by egg plantings and weather. *Ibid.*, **16**: 39–50.

PRITCHARD, A. L. 1929. The alewife (*Pomolobus pseudoharengus*) in Lake Ontario. *Univ. Toronto Stud., Biol., Ser.*, No. 38, pp. 38–54.

RICKER, W. E. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. *J. Fish. Res. Bd. Canada*, **15**(5): 991–1006.

SHEPARD, M. P., AND F. C. WITHLER. 1958. Spawning stock size and resultant production for Skeena sockeye. *Ibid.*, **15**(5): 1007–1025.

SMITH, EMIL J., JR. 1961. A mechanical net-puller for skiff fishing with gill nets. *California Fish and Game*, **47**: 327–333.

SMITH, HUGH M. 1892. Report on an investigation of the fisheries of Lake Ontario. *Bull. U.S. Fish. Comm.*, **10**: 177–215. (Document No. 194.)

SNEDECOR, GEORGE W. 1956. Statistical Methods. Iowa State College Press, 5th ed., 534 pp.

VAN OOSTEN, JOHN. 1929. The life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. *Bull. U.S. Bur. Fish.*, **44**: 265–428.

1942. Relationship between the plantings of fry and production of whitefish in Lake Erie. *Trans. Am. Fish. Soc.*, **71**: 118–121.

VAN OOSTEN, JOHN, HILARY J. DEASON AND FRANK W. JOBES. 1934. A microprojection machine designed for the study of fish scales. *J. Cons. Expl. Mer*, **9**: 241–248.

VAN OOSTEN, JOHN, AND RALPH HILE. 1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill) in Lake Erie. *Trans. Am. Fish. Soc.*, **77**: 178–249.

TABLES I-XV

TABLE I. The Canadian Lake Ontario commercial whitefish catch — 1924–1960 (reported values in pounds).

Year	Bay of Quinte	Eastern Lake Ontario[a]	Lake Total	June through September % of Total
1924	798,812	2,052,452	2,652,400	
1925	531,148	1,510,853	1,925,700	
1926	459,844	1,431,619	1,820,800	
1927	491,341	1,269,453	1,503,200	
1928	413,387	958,584	1,068,300	
1929	337,207	748,433	843,000	
1930	202,698	481,573	551,900	
1931	169,034	443,306	525,800	
1932	95,072	348,606	418,200	
1933	157,986	390,737	473,500	
1934[a]	145,186	385,984	489,500	
1935	275,000	548,671	657,400	
1936	262,749	461,499	576,200	
1937	179,697	471,434	551,500	
1938	196,194	491,718	602,300	
1939	190,200	531,627	664,500	
1940	154,086	340,931	403,600	
1941	171,575	396,054	441,600	
1942	186,748	403,482	442,000	
1943	175,900	302,326	329,300	
1944	242,819	434,841	460,900	
1945	158,659	340,888	359,400	
1946	179,169	364,807	397,900	
1947	146,554	323,069	357,800	
1948	95,601	208,504	236,700	36.4
1949	105,097	203,714	218,600	33.1
1950	162,035	386,426	418,900	60.1
1951	143,859	352,386	385,300	39.7
1952	105,578	374,101	406,440	40.9
1953	58,320	163,093	187,588	36.6
1954	63,044	193,387	207,064	41.6
1955	81,526	304,170	314,273	47.1
1956	152,721	538,102	571,004	47.8
1957	98,041	291,901	301,769	36.9
1958	113,216	309,908	317,814	37.0
1959	113,271	186,822	321,382	51.6
1960	77,877	197,275	262,070	35.2
			Average	41.8

[a]Brighton to St. Lawrence River including the Bay of Quinte.

TABLE II. Whitefish fry plantings in the Bay of Quinte.

Year of planting	Plantings—millions of fry	Year of planting	Plantings—millions of fry
1924	126.0	1939	40.0
1925	58.0	1940	89.0
1926	90.5	1941	20.0
1927	208.2	1942	6.0
1928	146.7	1943	43.3
1929	142.0	1944	23.5
1930	103.4	1945	no planting
1931	102.0	1946	21.5
1932	65.4	1947	no planting
1933	134.7	1948	55.0
1934	126.8	1949	no planting
1935	112.0	1950	32.0
1936	105.1	1951	no planting
1937	51.0	1952	17.0
1938	99.1	1953	no planting
		1954	13.0

TABLE III. The annual sample of the summer whitefish catch.

Year	(1) Lifts examined	(2) Specimens aged	(3) June–Sept. est. total catch	(4) June–Sept. total fish examined	(5) Summer percent examined
	no.	*no.*	*no.*	*no.*	%
1944	84	1402			
1945	57	1237			
1946	98	1882			
1947	42	1781			
1948	56	1598	34,019	1598	4.7
1949	55	1313	26,505	1313	5.0
1950	44	2247	100,236	2247	2.2
1951	58	2172	67,250	2080	3.1
1952	37	1554	73,942	1557	2.1
1953	36	1204	29,708	1206	4.1
1954	47	2387	40,261	1959	4.9
1955	52	3366	72,138	2797	3.9
1956	69	5102	122,385	3345	2.7
1957	52	2387	60,013	1487	2.5
1958	48	2850	54,996	1665	3.0
1959	32	2074	71,909	1899	2.6
1960	46	1888	41,367	1433	3.5
					Average: 3.4

TABLE IV. Weighted percentage age composition estimates.

Year	Age III	IV	V	VI	VII	VIII	IX	X+	Average Age
1944	2.85	56.59	10.55	11.04	17.60	1.47	2.00	.47	4.99
1945	3.57	6.36	68.22	8.64	5.33	6.22	1.03	.62	5.32
1946	1.86	30.36	8.73	48.78	5.98	1.90	1.95	.44	5.42
1947	2.81	37.99	27.21	4.20	25.34	.67	.90	.80	5.21
1948	3.34	43.04	28.73	12.96	4.66	6.37	.52	.38	4.96
1949	8.93	11.58	52.58	15.36	6.48	.15	4.37	.55	5.20
1950	5.02	65.71	6.39	15.33	2.84	1.85	.70	2.03	4.64
1951	19.19	17.05	55.72	1.65	3.78	1.04	.49	1.08	4.64
1952	2.32	52.01	21.14	21.29	1.78	.51	.58	.37	4.74
1953	12.21	18.92	45.02	3.89	17.77	.43	.55	.99	5.05
1954	49.38	29.86	11.59	5.83	1.97	.82	.24	.16	3.85
1955	38.69	43.09	11.91	3.49	2.23	.10	.09	.40	3.90
1956	1.87	81.77	12.18	2.76	.58	.35	.15	.17	4.21
1957	32.31	8.78	50.62	5.36	.69	.34	.15	.35	4.36
1958	67.55	16.14	2.10	12.81	1.07	.29	.01	.03	3.65
1959	4.38	81.03	8.85	.90	4.14	.22	.06	.02	4.20
1960	53.58	5.08	34.13	3.13	.98	2.61			4.00
								Average 1944–49:	5.18
								Average 1950–60:	4.29

TABLE V. Estimated numbers of whitefish removed at various ages during the years 1944 to 1960.

Year	Age III	IV	V	VI	VII	VIII	IX	X+	Total fish*
1944	5,756	114,291	21,307	22,297	35,546	2969	4039	949	201,964
1945	5,337	9,508	101,989	12,917	7,968	9299	1540	927	149,500
1946	3,128	51,056	14,681	82,033	10,057	3195	3279	740	168,169
1947	4,132	55,861	40,010	6,176	37,260	985	1323	1176	147,042
1948	2,837	36,554	24,401	11,007	3,958	5410	442	323	84,931
1949	7,183	9,315	42,295	12,355	5,212	121	3515	442	80,437
1950	8,359	109,416	10,640	25,527	4,729	3081	1166	3380	166,514
1951	32,402	28,789	94,083	2,786	6,382	1756	827	1824	168,849
1952	4,198	94,118	38,255	38,527	3,221	923	1050	670	180,962
1953	9,915	15,364	36,559	3,159	14,430	349	447	804	81,207
1954	48,993	29,626	11,499	5,784	1,955	814	238	159	99,216
1955	58,486	65,137	18,004	5,276	3,371	151	136	605	151,165
1956	4,667	204,069	30,397	6,888	1,447	873	374	424	249,565
1957	42,154	11,455	66,042	6,993	900	444	196	457	130,466
1958	101,218	24,184	3,147	19,195	1,603	435	15	45	149,842
1959	5,681	105,091	11,478	1,167	5,369	285	78	26	129,694
1960	62,798	5,954	40,002	3,669	1,149	3059			177,205

*Total fish $= \frac{\text{Catch (lb)}}{\text{Average weight}}$. These are not always equal to the sum of the individual catches by age which are based on average percentages not always totalling to 100%.

TABLE VI. Virtual populations of Lake Ontario whitefish.

Year	Age							
	III	IV	V	VI	VII	VIII	IX	X+
1934								949
1935							4966	927
1936						5,249	2280	740
1937					49,300	13,754	4455	1176
1938				35,106	12,809	4,841	1646	323
1939			46,150	24,843	11,926	1,869	884	442
1940		347,878	233,587	131,598	49,565	12,305	6895	3380
1941	43,190	37,434	27,926	13,245	7,069	3,111	2990	1824
1942	117,200	111,863	60,807	20,797	9,790	4,578	1497	670
1943	104,084	100,956	45,095	20,694	8,339	3,610	1854	804
1944	116,419	112,287	75,733	33,438	7,911	1,529	606	159
1945	29,991	27,154	17,839	7,199	4,413	1,192	843	605
1946	265,013	257,830	148,414	54,331	15,804	1,374	560	424
1947	81,499	73,140	44,351	6,096	2,937	982	831	457
1948	173,348	140,946	46,828	10,269	4,485	1,114	241	45
1949	38,269	34,071	18,707	7,208	1,932	485	41	26
1950	65,846	55,931	26,305	8,301	1,413	513	78	
1951	153,408	104,415	39,278	8,881	1,888	285		
1952	356,670	298,184	94,115	28,073	8,878	3,509		
1953	21,585	16,918	5,463	2,316	1,149			
1954	81,485	39,331	15,147	3,669				
1955	246,311	145,093	40,002					
1956	11,635	5,954						
1957	62,798							

TABLE VII. Estimated whitefish year-class contributions to the fishery through ages III–VI and corresponding hatchery support.

Year-class	Whitefish caught (age III–VI)	Fry planted (millions)
	no.	
1938	(237,202)*	99.1
1939	(91,264)	40.0
1940	(351,370)	89.0
1941	36,121	20.0
1942	107,410	6.0
1943	95,745	43.3
1944	108,508	23.5
1945	25,578	0
1946	249,209	21.5
1947	78,562	0
1948	168,863	55.0
1949	36,337	0
1950	64,433	32.0
1951	151,520	0
1952	347,792	17.0
1953	20,436	0
1954	81,485	13.0
1955	(271,866)	0
1956	(18,616)	0
1957	(415,881)	0

*Values in parentheses are estimates extrapolated from incomplete contributions.

TABLE VIII. Summary of catch statistics for the Canadian waters of Lake Ontario — lake trout and whitefish.

Decade	Annual whitefish catch			Annual lake trout catch		
	Average	Maximum	Minimum	Average	Maximum	Minimum
	cwt	*cwt*	*cwt*	*cwt*	*cwt*	*cwt*
1860*	9187	11563	6590	4670	6127	3823
1870	6384	8231	4642	3022	4384	1184
1880	3892	7990	1310	2459	3816	967
1890	3328	6020	1267	1497	2397	1017
1900	3751	11533	790	1453	6398	601
1910	9365	15936	5179	5141	6330	3846
1920	18672	26524	8430	7359	10623	4621
1930	5511	6645	4182	2884	3882	2050
1940	3647	4609	2186	889	1874	215
1950	3385	5710	2071	254	402	138**

*Three years only, including some catches from Lake Erie.
**Four years only.

TABLE IX. Deviations* from trend in the catch and planting statistics.

Year	x' catch series	y fry planting series	Year	x' catch series	y fry planting series
1925	−12.8	−61.1	1943	− 9.4	37.6
1926	30.3	35.7	1944	12.2	−17.4
1927	6.3	122.7	1945	− 7.8	0
1928	−13.8	−50.1	1946	3.6	− 0.7
1929	− 4.2	3.3	1947	− 3.2	0
1930	−16.7	−30.8	1948	−12.4	34.7
1931	2.2	4.3	1949	− 5.3	0
1932	− 6.6	−31.0	1950	16.1	−20.0
1933	6.9	72.9	1951	− 2.1	0
1934	4.4	− 0.5	1952	2.5	−13.2
1935	19.9	− 7.9	1953	−20.8	0
1936	− 0.5	− 0.8	1954	− 2.8	− 3.1
1937	3.0	−48.3	1955	6.5	0
1938	9.8	50.9	1956	24.3	0
1939	12.4	−53.7	1957	−21.6	0
1940	−18.3	51.2	1958	− 0.1	0
1941	4.7	−64.1	1959	− 1.0	0
1942	1.9	−12.9	1960	− 7.1	0

*See text for derivations.

TABLE X. Air temperature data Bay of Quinte area.

Year	Deviations* from mean		Thermal** index	Year	Deviations* from mean		Thermal** index
	April	*Nov.*			*April*	*Nov.*	
1924	− .7	0		1941	+5.1	+2.4	+6.5
1925	+ .3	−1	+ .3	1942	+5.7	− .5	+3.3
1926	−6.7	0	−5.7	1943	−6.2	−1.0	−5.7
1927	+ .3	+1.0	+ .3	1944	−3.5	+ .3	−2.5
1928	−4.7	+1.0	−5.7	1945	+4.2	0	+3.9
1929	+2.3	0	+1.3	1946	+ .3	+3.4	+ .3
1930	− .7	+2.0	− .7	1947	−2.3	−2.0	−5.7
1931	+2.3	+6.0	+ .3	1948	+2.9	+6.2	+4.9
1932	−2.7	−3.0	−8.7	1949	+1.1	−4.0	−5.1
1933	+2.3	−9.0	+5.3	1950	−4.7	+ .6	− .7
1934	−1.7	+3.0	+7.3	1951	+1.7	−5.7	+1.1
1935	+ .8	+1.2	−2.2	1952	+4.5	+3.6	+10.2
1936	−2.7	−5.7	−3.9	1953	+1.1	+4.6	−2.5
1937	+ .1	+ .8	+5.8	1954	+1.9	+1.6	−2.7
1938	+1.7	+ .8	+ .9	1955	+5.9	−1.8	+4.3
1939	−3.8	−4.2	−4.6	1956	−3.1	+1.7	−1.3
1940	−3.1	−1.4	+1.1	1957	+3.1	+2.3	+1.4

*34-year April average, 42.7°F; 33-year Nov. average, 37.0°F.
**Thermal index = April (year n), Nov. (year n−1).

TABLE XI. Hay Bay spawning run age and sex composition.

Spawning run		Fish caught at age						
		II	III	IV	V	VI	VII+	Total
		no.	*no.*	*no.*	*no.*	*no.*	*no.*	
1953	Male	4	47	40	39	8	6	145
	Female		7	10	43	11	15	87
	Total	10	113	88	144	32	34	425
1954	Male	106	770	231	40	16	2	1201
	Female		149	98	23	17	2	308
	Total	108	928	337	67	34	4	1531
1955	Male	2	196	95	37	7	7	384
	Female		74	87	35	17	12	243
	Total	2	277	184	73	24	19	637
1956	Male	3	10	143	22	12	2	217
	Female		4	50	18	11	6	100
	Total	4	14	196	41	23	8	323
1957	Male	12	46	4	23	1	1	93
	Female	1	3	1	20		2	28
	Total	14	50	5	48	1	3	130
1958	Male		121	15	4	7		150
	Female		33	2		5		40
	Total		170	19	4	14		212
All years	Male	127	1190	528	165	51	18	2079
	Female	1	270	248	139	61	37	756
	Total	138	1552	829	377	128	68	3092
Average male (%)		92.0	76.7	63.7	43.8	39.8	26.5	
Average female (%)		8.0	23.3	36.3	56.2	60.2	73.5	

TABLE XII. Estimation of spawning escapement.

	Fall virtual populations				
	(1)	(2)	(3)	(4)	(5)
Spawning year	Age III and older	Age V and older	Mature females	Weight mature females	Min. spawn potential $\times 10^6$ eggs
	no.	*no.*	*no.*	*lb*	
1943	489,598	95,570	88,000	200,000	2000
1944	325,634	54,613	77,646	185,049	1851
1945	293,349	153,560	100,588	237,932	2379
1946	229,264	67,501	57,893	132,653	1327
1947	198,760	41,378	40,998	99,655	997
1948	143,819	40,932	40,270	97,853	979
1949	328,394	52,725	51,500	118,892	1190
1950	243,595	22,041	44,704	102,804	1028
1951	249,094	62,797	52,996	121,292	1213
1952	105,401	24,502	25,275	58,199	582
1953	90,220	15,582	16,158	37,081	371
1954	144,560	13,840	19,641	43,356	434
1955	350,064	12,602	33,566	69,862	699
1956	122,510	11,477	24,358	54,889	549
Average:	236,740	47,794	48,114	111,394	1114
				Average for plant years:	1358
				Average plant:	27.0

TABLE XIII. Recruits per spawner year-class.

	Progeny from parent year-class at age					
Spawning year	III	IV	V	VI	VII+	Total produced year-class
1943	22,353	9,657	25,174	37,110	14,215	108,508
1944	614	12,508	4,527	2,455	5,474	25,578
1945	13,956	11,214	182,171	17,195	24,672	249,209
1946	7,071	13,984	10,370	40,695	6,521	78,562
1947	22,459	29,551	46,606	16,549	53,530	168,863
1948	1,199	10,901	10,138	5,051	9,084	36,337
1949	16,559	3,737	23,969	6,250	13,918	64,433
1950	12,728	84,700	14,091	16,213	23,940	151,520
1951	47,995	49,386	205,893	17,390	27,128	347,792
1952	1,410	6,376	2,820	7,684	2,146	20,436
1953	14,586	15,890	29,824	8,963	12,223	81,485
1954	77,482	63,889	59,811	38,877	31,536	271,866
1955	9,438	4,058	2,923	707	1,471	18,616
1956	14,972	276,145	88,999	14,972	20,794	415,881

TABLE XIV. Estimates of year-class strength with their respective numbers of progeny contributed to subsequent year-classes.

Year-class	Estimated initial strength	Estimated total progeny	Progeny per recruit
1940	351,370	311,257	0.89
1941	36,121	47,831	1.32
1942	107,410	93,515	0.87
1943	95,745	76,950	0.80
1944	108,508	100,670	0.93
1945	25,578	38,563	1.51
1946	249,209	327,059	1.31
1947	78,562	105,433	1.34
1948	168,863	124,543	0.74
1949	36,337	98,612	2.71
Average:	125,770	132,443	1.05

TABLE XV. Statistics of natural reproduction.

Year-class	Minimum spawn potential preceding fall $\times 10^6$ eggs	Ratios — Recruits / Million eggs: Thermal index negative	Thermal index positive
1944	2000	54.3	—
1945	1851	—	13.8
1946	2379	—	104.8
1947	1327	59.2	—
1948	997	—	169.4
1949	979	37.1	—
1950	1190	54.1	—
1951	1028	—	147.4
1952	1213	—	286.7
1953	582	35.1	—
1954	371	219.6	—
1955	434	—	626.4
1956	699	26.6	—
1957	549	—	757.5
	Average excl. 1954	44.4	Average excl. 1945 348.7
	Average supported year-classes	109.3	187.0
	Average unsupported year-classes	39.5	386.3

Interspecific Competition and Exploitation[1,2]

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ABSTRACT

The consequences of exploitation of either or both of a pair of competing species are examined using the Lotka-Volterra equations. The removal of a fixed proportion of a population on an instantaneous basis shifts the equilibrium population sizes for both the exploited species and its competitor. Similar shifts occur when both species are exploited. The maximum sustained yield of a species can be estimated under various degrees of exploitation of its competitor. The maximum combined sustained yield can be estimated for various relative values of the two species. From this analysis it is observed (1) harvesting only one species may provide a mistaken underestimate of capacity for sustained yield, (2) harvesting two species but relating yield to the fishing mortality rate of only one of the two may give a misleading overestimate of further capacity for sustained yield. Similar conclusions can be drawn if exploitation rate is proportional to abundance.

A stochastic version of the model is given for study of the effects of exploitation on small populations of competitors.

Fixed percentage exploitation and abundance proportional exploitation may be considered as depicting respectively the mode of action of density-independent and density-dependent factors. Accepting these parallels, the model may demonstrate some widely discussed properties of mechanisms of population regulation. Variability in factors both density dependent and density independent which are extrinsic to the biological system can be simulated in the model by random variates.

A discrete time model is described which was used with a computer for study of transitions from one steady state to another and extinction probabilities. The computer results confirm the theoretical predictions of the model. In addition it is suggested that there is no apparent difference in the result when competitors are exposed to the same or different random sequences of environmental effects of the same average intensity.

It is concluded that this formulation of interspecific competition together with variations should be applied to laboratory or natural situations to test its usefulness as a basis for prediction.

INTRODUCTION

The likelihood that interspecific competition may be a factor in the yield obtained from exploited stocks of fishes has been recognized in many publications. Despite the general acceptance of the phenomenon, there is a paucity of theoretical models on which to base expectations of yield where interspecific competition is involved. Beverton and Holt (1957) developed a form of model consistent with their general scheme for study of exploited populations; a model in which com-

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petition is between species feeding exclusively on a common supply. They also describe the formulation of Shorygin (1946) for the case of two predator populations sharing a common prey, suggesting modifications that might make the model more realistic. Ricker (1958a) has examined the consequences of a fishery which exploits mixed (but not interacting) stocks characterized by different reproductive curves. Except for these few isolated instances there are few models to which field data may be compared when interspecific competition is "suspect" as a factor influencing yield.

The emphasis on "suspicion" of interspecific competition is pertinent both to the practical problems of investigation in natural conditions and the choice of an appropriate mathematical model. Circumstantial evidence of competition is commonly reported, but there are few instances in which the mechanisms involved have been demonstrated (Larkin, 1954). This is hardly surprising considering the difficulties involved in even a simple natural situation. Without the opportunity for observation of the consequences of introduction of a competitor, it may not be apparent from superficial study that competition even occurs (Johannes and Larkin, 1960). There is also the possibility that the influence of one species on another may be mediated in a complex for which the total effect is measurable, but in which precise formulation of mechanisms involved would be formidable (for example the well known examples of competition between populations of stored products insects).

In these circumstances there are two sides to the question of a suitable choice of mathematical model. It may be preferable in the words of Beverton and Holt (1957) "to develop models according to the properties of particular systems" and to develop generalisations as they "emerge as syntheses of knowledge of a range of actual cases . . .". On the other hand, where knowledge of the real processes is difficult to obtain, there would seem to be advantage in a general associative type of model at least as a working basis for study. Moreover, the associative model can be constructed on the grounds of mathematical convenience, whereas the mechanistic model may pay for its biological realism by being unrealistic in its demand for data and appropriate mathematical techniques of analysis.

With these thoughts in mind, the present study develops the consequences of exploitation in associations of competing species as they are represented in the Lotka-Volterra equations (cf. Brian, 1956, regarding "Winsor"-type equations). The situations described may have no counterpart in nature so far as fish populations are concerned. It is pertinent to mention that some success in applying the Volterra equations to the problems raised by laboratory populations has been achieved by Leslie and his associates (Leslie, 1958, 1962; Leslie and Gower, 1958, 1960), and some of the phenomena here described have on occasion had laboratory confirmation.

The equations of Lotka and Volterra belong to the logistic "family", which have an historical application to fisheries biology (D'Ancona, 1942; Graham, 1939). In this respect, the observations which follow can be considered an extension of the logistic theory to two species systems under exploitation.

THE DETERMINISTIC MODEL

The Lotka-Volterra equations for two competing species are:

$$\frac{dN_1}{dt} = r_1N_1 - a_1N_1^2 - b_1N_1N_2$$

$$\frac{dN_2}{dt} = r_2N_2 - a_2N_2^2 - b_2N_1N_2 \qquad (1)$$

where r_i $(i = 1,2)$ is the intrinsic rate of increase which would be approached if no limitations were placed on the increase in numbers of the respective populations if they were living alone; and where $r_i = b_i' - d_i$ the difference between the birth rate (b') and death rate (d) under these conditions.

The parameters a_i $(i = 1, 2)$ must be greater than 0 and represent intraspecific checks on rates of increase, and the asymptotic population size of each species living alone is given by $K_i = \frac{r_i}{a_i}$

The coefficients b_i $(i = 1, 2)$ provide for the effects of each species on its competitor and by definition are greater than 0. The ratio b_i/a_i gives the effect of a competitor species in relation to the effect a species has on itself. Setting $K_i = r_i/a_i$ and $k_i = b_i/a_i$ equations (1) may also be written in the familiar alternative form:

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 - N_1 - k_1N_2}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2 - k_2N_1}{K_2}\right) \qquad (1A)$$

The system described by equations (1) will have a stationary state when:

$$\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$$

or when:

$$N_1 = L_1 = \frac{a_2r_1 - b_1r_2}{a_1a_2 - b_1b_2}$$

$$N_2 = L_2 = \frac{a_1r_2 - b_2r_1}{a_1a_2 - b_1b_2} \qquad (2)$$

The relative values of the a_i, b_i and r_i determine whether both L_1, $L_2 > 0$ and if so, whether the equilibrium is stable or unstable. The system may have four states:

$\frac{b_1b_2}{a_1a_2} > \frac{b_1r_2}{a_2r_1} < 1$ species 1 persists

$\frac{b_1b_2}{a_1a_2} < \frac{b_1r_2}{a_2r_1} > 1$ species 2 persists

$\frac{b_1b_2}{a_1a_2} < \frac{b_1r_2}{a_2r_1} < 1$ stable equilibrium; both species persist

$\frac{b_1b_2}{a_1a_2} > \frac{b_1r_2}{a_2r_1} > 1$ unstable equilibrium; one species persists, the result depending on initial numbers

Fixed Percentage Exploitation

The removal of a fixed proportion of the population on an instantaneous basis may be incorporated in equations (1) by adding to the right hand side the term $-c_i N_i$. This term can be grouped with $r_i N_i$ and the expression $r_i - c_i$ can be denoted as r_i'. Thus:

$$\frac{dN_1}{dt} = r_1' N_1 - a_1 N_1^2 - b_1 N_1 N_2$$

$$\frac{dN_2}{dt} = r_2' N_2 - a_2 N_2^2 - b_2 N_1 N_2 \qquad (3)$$

It follows that if only one species is exploited, then:

$$\text{if } r_1' < \frac{b_1 r_2}{a_2} \quad \text{species 2 only persists}$$

$$\text{if } r_2' < \frac{b_2 r_1}{a_1} \quad \text{species 1 only persists.}$$

If both species are exploited, then:

$$\text{if } \frac{b_1}{a_2} > \frac{r_1'}{r_2'} < \frac{a_1}{b_2} \quad \text{species 2 only persists}$$

$$\text{if } \frac{b_1}{a_2} < \frac{r_1'}{r_2'} > \frac{a_1}{b_2} \quad \text{species 1 only persists}$$

$$\text{if } \frac{b_1}{a_2} < \frac{r_1'}{r_2'} < \frac{a_1}{b_2} \quad \text{both species persist.}$$

These relationships are summarized for a particular example in Fig. 1, which illustrates the displacement of equilibrium resulting from exploitation of either

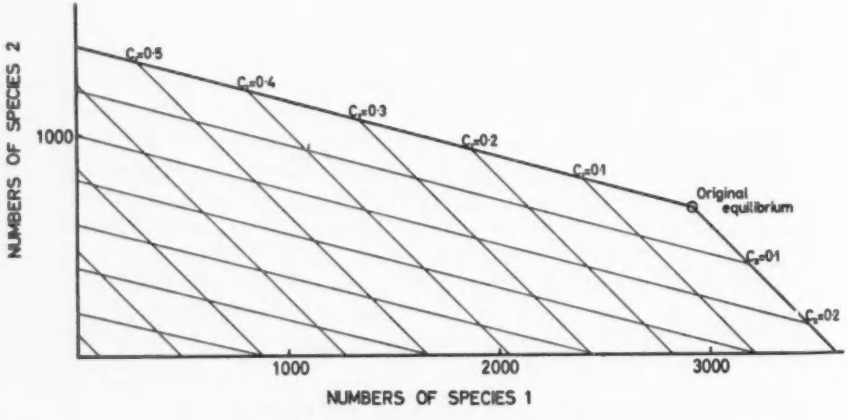

FIG. 1. Displacement from original equilibrium in relation to various rates of fixed percentage instantaneous fishing mortality. For example, with $c_1 = 0.4$ and $c_2 = 0.2$ equilibrium is at $N_1 = 1333$, $N_2 = 667$.

or both species at a fixed percentage instantaneous rate[4]. In this example (which will be used throughout this paper) the values of the parameters are:

$$r_1 = 0.9 \qquad a_1 = .00025 \qquad b_1 = .00025$$
$$r_2 = 0.7 \qquad a_2 = .00050 \qquad b_2 = .000125$$

These particular values are convenient for an example because at an unexploited equilibrium there are 2933 individuals of species 1 and 667 of species 2, a disproportion which makes available comparison of the effects of exploiting either the "dominant" or "subordinate" species of a competing pair. When species 1 is exploited at a rate of $c_1 = 0.2$ and $c_2 = 0$ then equilibrium is displaced to $N_1 = 1868$, $N_2 = 934$. Species 1 is eliminated when $c_1 = 0.55$ and species 2 persists at the abundance appropriate to its existence as a single species population ($N_2 = 1400$). Similarly species 1 only persists at $N_1 = 3600$ when species 2 is exploited at a rate of $c_2 = 0.25$ and $c_1 = 0$. When both species are exploited at the rates $c_1 = 0.55$, $c_2 = 0.25$ then both persist with $N_1 = 667$, $N_2 = 733$.

The formulae of any pair of intersecting straight lines which define an equilibrium can be obtained by rearranging and simplifying equations (2) when r_i' is substituted for r_i. Thus:

$$N_1 = L_1' = \frac{r_2' - a_2 L_2'}{b_2}$$

$$N_2 = L_2' = \frac{r_1' - a_1 L_1'}{b_1} \tag{4}$$

The yield or catch which results from exploitation will be sustained when $c_i N_i = dN_i/dt$ $(i = 1, 2)$ of equations (3) and where N_1 and N_2 are in equilibrium. Equations (3) can be used to determine the equilibrium situation which maximizes the yield of one species when the level of exploitation or the population size of the other is fixed.

Thus, to obtain the maximum yield (Y) from species 1 for a *given* fixed rate of "fishing" mortality of species 2, we may write:

$$Y = c_1 N_1$$

But N_1 and N_2 must be in equilibrium. Hence N_1 will be given by equation (2) with r_1 replaced by $r_1 - c_1$ and r_2 replaced by $r_2 - c_2$. Substituting we have:

$$Y_1 = c_1 \left\{ \frac{a_2(r_1 - c_1) - b_1(r_2 - c_2)}{a_1 a_2 - b_1 b_2} \right\} \tag{5}$$

[4]Alternatively, the equilibrium values of N_1 and N_2 can be plotted on the axes c_1 and c_2. Dr D. G. Chapman has pointed out that the inequality:

$$\frac{b_1}{a_2} < \frac{r_1 - c_1}{r_2 - c_2} < \frac{a_1}{b_2}$$

can be solved for the inequalities in c_1, c_2, viz.:

$$a_2 c_1 - b_1 c_2 < a_2 r_1 - b_1 r_2$$
$$-b_2 c_1 + a_1 c_2 < a_1 r_2 - b_2 r_1$$

Replacing $<$ by $=$, gives the formulae for the pair of lines marking the zone of stability in the c_1, c_2 plane.

Differentiating and equating to 0, yield of species 1 is maximum for a given rate of fishing mortality for species 2 where:

$$c_1 = \frac{(a_2r_1 - b_1r_2) + c_2b_1}{2a_2} \tag{6}$$

provided that species 2 is not eliminated.

Similarly yield for species 2 is maximum, provided species 1 is not eliminated, where:

$$c_2 = \frac{(a_1r_2 - b_2r_1) + c_1b_2}{2a_1} \tag{7}$$

The combination of fishing mortality rates at which yield is maximum for *each* species (i.e. the point at which any change in exploitation decreases the yield of either one or the other species) can be shown empirically to be slightly closer to the origin than the intersection of the two lines which describe maximum yield of each species for given fishing mortality rate of its competitor. This anomaly is related to the implicit nature of equations (1) and the simplification of fixed values introduced for the purposes of obtaining equations (6) and (7).

The point of *combined* maximum yield can be obtained precisely using partial derivatives. In similar fashion to equation (5) we may write:

$$Y_1 + Y_2 = c_1\left\{\frac{a_2(r_1 - c_1) - b_1(r_2 - c_2)}{a_1a_2 - b_1b_2}\right\} + c_2\left\{\frac{a_1(r_2 - c_2) - b_2(r_1 - c_1)}{a_1a_2 - b_1b_2}\right\} \tag{8}$$

Simplifying:

$$Y_1 + Y_2 = \frac{c_1(a_2r_1 - b_1r_2) - c_1^2a_2 + c_2(a_1r_2 - b_2r_1) - c_2^2a_1 + c_1c_2(b_1 + b_2)}{a_1a_2 - b_1b_2}$$

Taking partial derivatives, equating to zero and solving simultaneously, the combined maximum sustained yield is realized where:

$$c_1 = \frac{2a_1a_2r_1 - a_1r_2(b_1 - b_2) - b_2r_1(b_1 + b_2)}{4a_1a_2 - (b_1 + b_2)^2}$$

$$c_2 = \frac{2a_1a_2r_2 - a_2r_1(b_2 - b_1) - b_1r_2(b_1 + b_2)}{4a_1a_2 - (b_1 + b_2)^2} \tag{9}$$

In some situations, it may be appropriate to calculate maximum yields for various fixed levels of abundance of the competitor rather than for various fixed rates of its fishing mortality. By equating the derivatives of the right hand sides of equations (1) to 0 the yield of species 1 for various values of N_2 is maximum where:

$$N_1 = \frac{r_1 - b_1N_2}{2a_1} \tag{10}$$

Similarly the yield of species 2 is maximum where:

$$N_2 = \frac{r_2 - b_2N_1}{2a_2} \tag{11}$$

Again, the intersection of these lines does not give the point of maximum yield of *each* species because of the "fixed" value simplification.

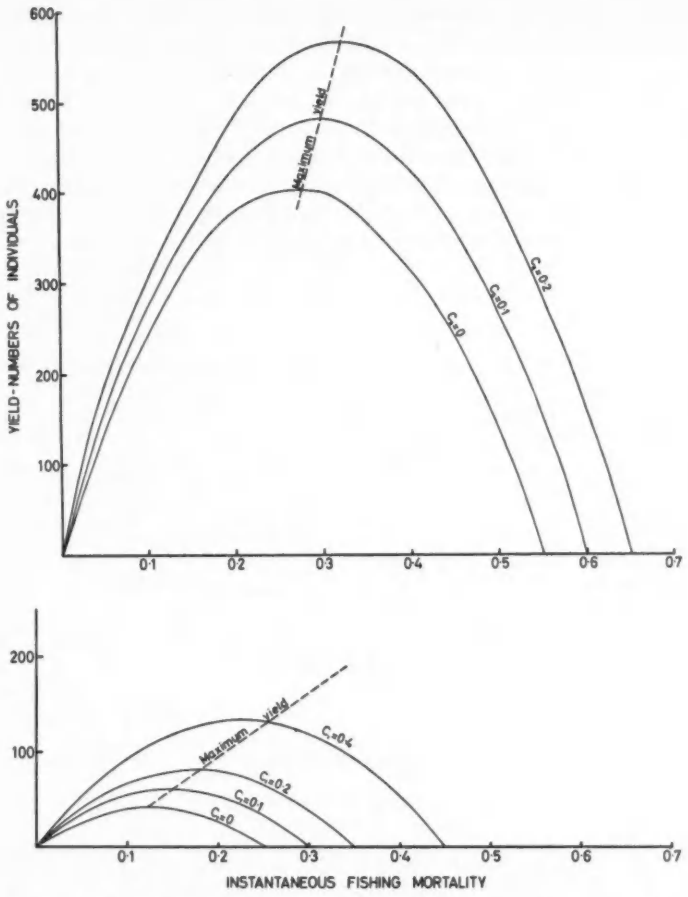

FIG. 2. *Above*: Yield of species 1 in relation to instantaneous fishing mortality at various levels of fishing species 2. *Below*: Yield of species 2 in relation to instantaneous fishing mortality at various levels of fishing species 1.

Taking partial derivatives of the sum of the right hand sides of equations (1), equating to 0, and solving simultaneously provides the precise values of N_1 and N_2 associated with combined maximum yield:

$$N_1 = \frac{2a_2r_1 - r_2(b_1 + b_2)}{4a_1a_2 - (b_1 + b_2)^2}$$

$$N_2 = \frac{2a_1r_2 - r_1(b_1 + b_2)}{4a_1a_2 - (b_1 + b_2)^2} \qquad (12)$$

Equations (12) may also be derived by substituting equations (9) in equations (2) which specify equilibrium.

Sustained yields for various levels of exploitation follow the familiar symmetrical dome-shaped curve (Fig. 2) with the added feature that yields are greater for either species when its competitor is also exploited. Thus species 1 in the example above when harvested alone will sustain a maximum yield of 403 individuals at $c_1 = 0.275$ compared to 563 at $c_1 = 0.325$ when species 2 is exploited at a rate $c_2 = 0.2$ Isopleths of yield at various equilibria (which correspond to various fishing mortality rates) illustrate this kind of example over the whole range of exploitation rates (Fig. 3). Species 2 is evidently less productive than species 1, although more responsive to exploitation of its competitor, reflecting

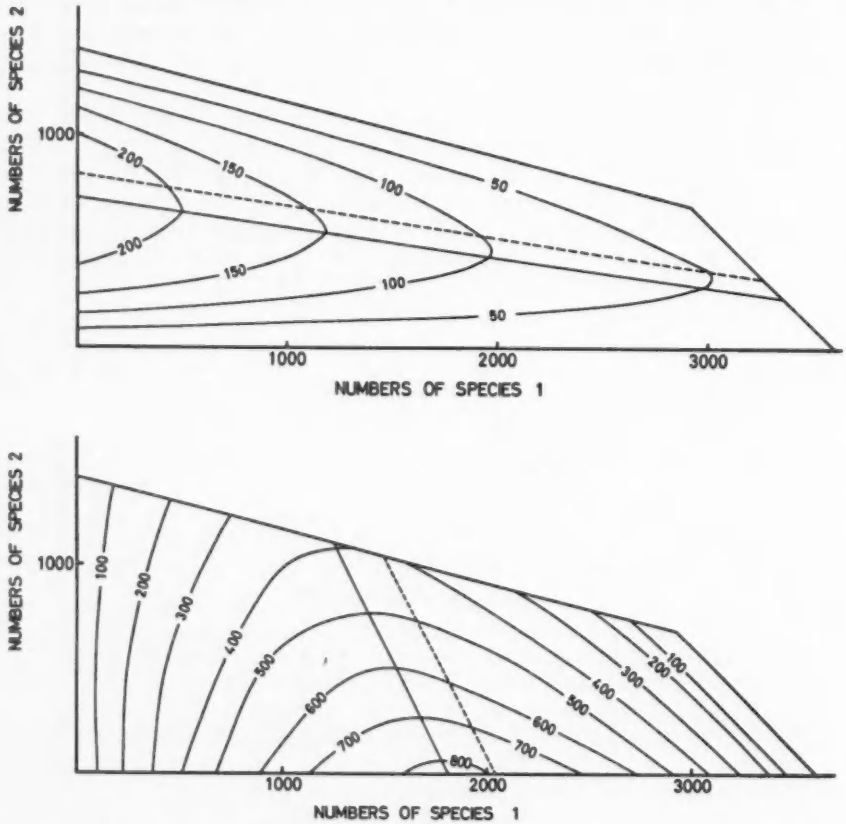

FIG. 3. *Above*: Isopleths of yield of species 1 at various equilibria with species 2. The solid line gives the maximum sustained yield of species 1 for any given fixed number of species 2. The dotted line gives the maximum sustained yield of species 1 for any given rate of fishing mortality of species 2. *Below*: Isopleths of yield of species 2 at various equilibria with species 1. The solid line gives maximum sustained yield for species 2 for any given fixed number of species 1. The dotted line gives the maximum sustained yield of species 2 for any given rate of fishing mortality of species 1.

the initial choice of parameters for the two species. It is reiterated that these estimates of yield are all approximate because they are based on derivations obtained from considering that the competitor species has fixed N or c. The isopleths of combined yield of the two species (Fig. 4) are a series of curves centred on a locus just within the zone in which neither species is eliminated ($N_1 = 1773.91$, $N_2 = 34.78$) where the combined yield is 810.4 individuals. The position of the locus reflects the initial choice of parameters and need not necessarily be very near to one of the axes. For instance, when:

$$\begin{array}{lll} r_1 = 1.0 & a_1 = .0005 & b_1 = .0003 \\ r_2 = 1.0 & a_2 = .0004 & b_2 = .0004 \\ & L_1 = L_2 = 1250 & \end{array}$$

combined yield is maximum where $N_1 = 323$, $N_2 = 968$.

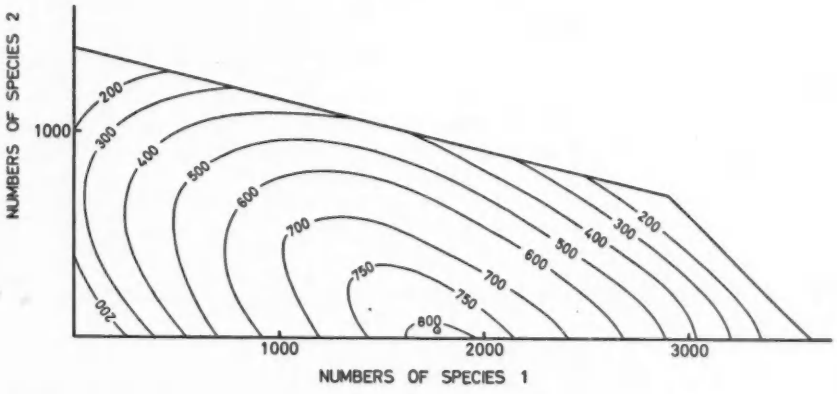

FIG. 4. Combined sustained yield of species 1 and species 2 at various equilibria. Combined maximum sustained yield is at $N_1 = 1773.9$, $N_2 = 34.8$.

The point of combined maximum yield may also be substantially influenced when some relative value is placed on the catch of each species. Following the procedure leading to equations (9) it can be demonstrated that if V is taken as the ratio of the value of species 2 to the value of species 1, then the combined maximum value of yield is attained where:

$$c_1 = V\,\frac{[2a_1a_2r_1 - a_1r_2(b_1 - Vb_2) - b_2r_1(b_1 + Vb_2)]}{4Va_1a_2 - (b_1 + Vb_2)^2}$$

$$c_2 = \frac{2a_1a_2r_2 - a_2r_1(b_2V - b_1) - b_1r_2(b_1 + Vb_2)}{4Va_1a_2 - (b_1 + Vb_2)^2}$$

If $V = 2.0$ (species 2 twice as valuable as species 1), the combined maximum value yield is attained where $c_1 = 0.45$, $c_2 = 0.18$ and the population levels are $N_1 = 1022$, $N_2 = 777$.

The foregoing analysis of yield in competitive situations contains two implications for management. (1) Harvesting only one species may provide a mistaken underestimate of capacity for sustained yield. Exploitation of the competitor species might prove an economical measure if carried on only to enable a greater harvest of the species of first interest. (2) Harvesting two species but relating yield to the fishing mortality rate of only one of the two may in some situations give a misleading overestimate of further capacity for sustained yield. In Fig. 5, yield for a given species is plotted against the fishing mortality rate when the competitor is exploited at various proportional rates (e.g. $c_1 = 0.5c_2$). If one species is eliminated the yield curve for the survivor may be quite asymmetrical, and in all cases the yield which can be sustained is dependent upon exploitation of the competitor. Thus if the exploitation of species 2 should cease, the yield which species 1 would sustain at $c_1 = 0.5$ would drop from 467 to 133 (upper panel of Fig. 5, line A). Similarly if the exploitation of species 1 should cease when $c_1 = c_2 = 0.3$ then species 2 is eliminated instead of maintaining a yield of 80 individuals (lower panel of Fig. 5, line B). The development of a gear more selective of a desired species than of its competitors might thus have substantial undesired effects on yield.

The foregoing analysis of fixed percentage exploitation can be related directly to the methods of Graham as described and adapted by Ricker (1958b). Graham's postulate of equilibrium yield may be written:

$$pW = W\left\{\frac{k(W_\infty - W)}{W_\infty}\right\}$$

Dealing in weight rather than numbers we may write equations (3) in the form, say for species 1:

$$\frac{dW_1}{dt} = r_1W_1 - c_1W_1 - a_1W_1^2 - b_1W_1W_2 \tag{13}$$

Setting $W_\infty = r_1/a_1$ and specifying that for equilibrium $cW = dW/dt$ we have after a little rearranging:

$$c_1W_1 = W_1\left\{\frac{r_1(W_\infty - W_1 - b_1W_2)}{W_\infty}\right\} \tag{14}$$

which is a simple modification of the Graham equation.

Exploitation Rate Proportional to Abundance

The removal of a variable fraction of the population which is proportional to the size of the population can be depicted by adding to the right hand side of equation (1) the term $-s_iN_i^2$ $(i = 1, 2)$. Thus, for species 1 say:

$$\frac{dN_1}{dt} = r_1N_1 - a_1N_1^2 - s_1N_1^2 - b_1N_1N_2 \tag{15}$$

$$\text{or: } \frac{dN_1}{dt} = r_1N_1 - a_1'N_1^2 - b_1N_1N_2 \tag{16}$$

where $a_1' = a_1 + s_1$. If only species 1 is exploited then the equilibrium level for both species will shift to:

$$N_1 = L_1 = \frac{a_2 r_1 - b_1 r_2}{a_1' a_2 - b_1 b_2}$$

$$N_2 = L_2 = \frac{a_1' r_2 - b_2 r_1}{a_1' a_2 - b_1 b_2} \qquad (17)$$

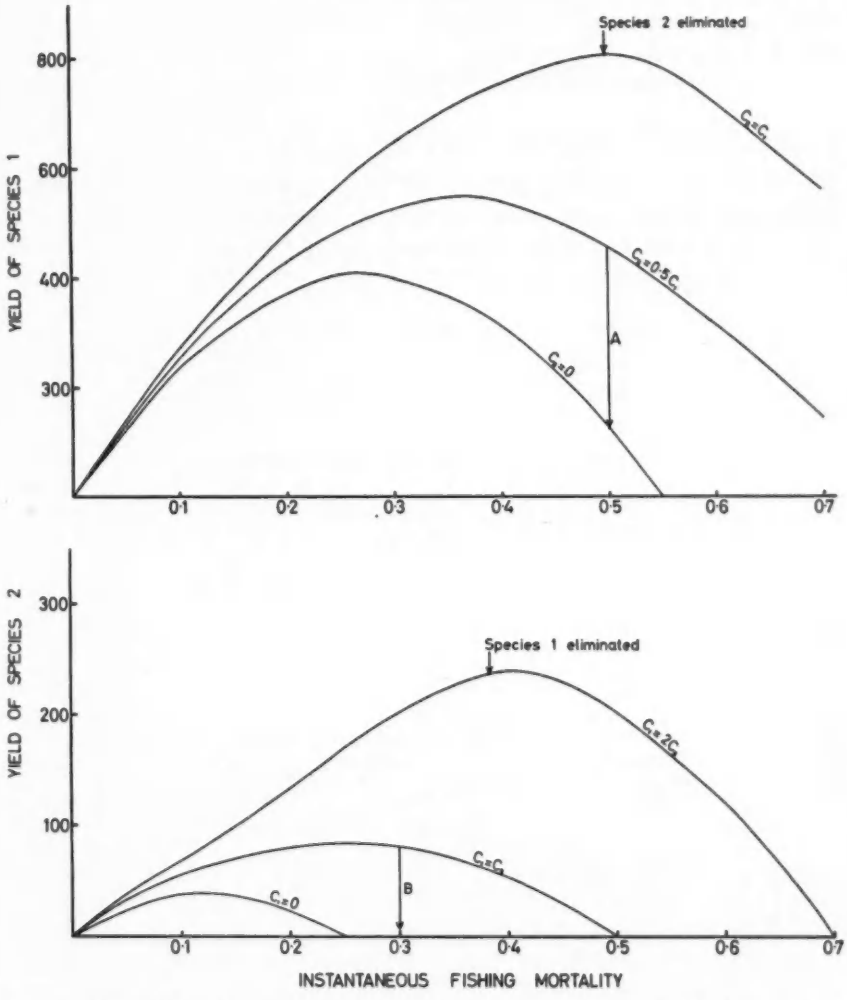

FIG. 5. *Above*: Yield of species 1 in relation to instantaneous fishing mortality when species 2 is harvested at various rates in relation to species 1. *Below*: Yield of species 2 in relation to instantaneous fishing mortality when species 1 is harvested at various rates in relation to species 2.

This kind of exploitation will not "eliminate" a species unless "fractions" of animals are disregarded and then only where the denominator of (17) becomes larger than the numerator, in which case $L_1' < 1$. The same is true if both species are exploited.

Alternatively, exploitation may be depicted by two terms in equation (15), a base rate of a fixed percentage fishing mortality, $c_i N_i$, to which is added another component that is proportional to abundance, $s_i N_i^2$. In this case, representing $(r_i - c_i)$ as r_i' and $(a_i + s_i)$ as a_i', when only one species is exploited then:

$$\text{if } r_1' < \frac{b_1 r_2}{a_2} \quad \text{species 2 only persists}$$

$$\text{if } r_2' < \frac{b_2 r_1}{a_1} \quad \text{species 1 only persists.}$$

This type of exploitation shares the properties of fixed and proportional exploitation, as one would expect; the same c_i are required for elimination as in the fixed exploitation, and the values s_i only change the positions of equilibrium. The same is true when both species are exploited. In this instance:

$$\text{if } \frac{a_2' r_1'}{r_2'} < b_1 \text{ and } \frac{a_1' r_2'}{r_1'} > b_2 \quad \text{species 2 only persists}$$

$$\text{if } \frac{a_2' r_1'}{r_2'} > b_1 \text{ and } \frac{a_1' r_2'}{r_1'} < b_2 \quad \text{species 1 only persists}$$

$$\text{if } \frac{a_2' r_1'}{r_2'} > b_1 \text{ and } \frac{a_1' r_2'}{r_1'} > b_2 \quad \text{both species persist}$$

$$\text{if } \frac{a_2' r_1'}{r_2'} < b_1 \text{ and } \frac{a_1' r_2'}{r_1'} < b_2 \quad \text{one species persists depending on the initial numbers.}$$

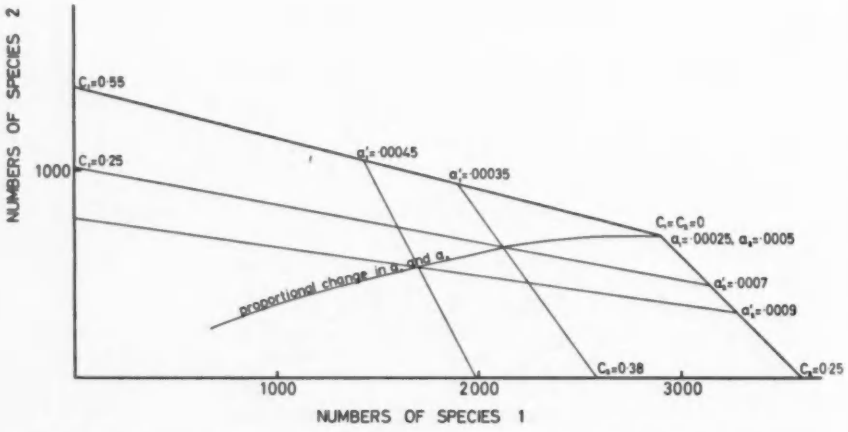

FIG. 6. Displacement from original equilibrium in relation to various rates of exploitation in proportion to abundance. For example, if $a_1' = 0.00035$ ($s_1 = 0.00010$), equilibrium is at $N_1 = 1915$, $N_2 = 923$; for extinction of species 1, $c_1 = 0.55$, and for extinction of species 2, $c = 0.38$.

The fourth alternative is not a real possibility in this model because the initial system assumed that $b_1b_2 < a_1a_2$ and increasing a_i by s_i preserves this inequality. Later reference will be made to this case which has interest as a potential situation from which a stable state may result from exploitation.

Figure 6 illustrates the changes in equilibria resulting from exploitation in relation to abundance, using the same example as previously.

With increase in a_1 to 0.00035 ($s_1 = 0.00010$), equilibrium is displaced to about the same extent as with $c_1 = 0.2$. In conformity with the inequalities given above, change in a_1 does not influence the value of c_1 required to eliminate species 1 (i.e. $c_1 = 0.55$), but does change the value of c_2 required to eliminate species 2 (from $c_2 = 0.25$ to $c_2 = 0.38$).

The equilibrium levels associated with yield maxima for exploitation in relation to abundance are the same as for fixed percentage exploitation, (for $s_iN_i^2 = c_iN_i = \frac{dN_i}{dt}$) and the appropriate formulae may be derived in similar fashion. Thus for fixed values of s_2 yield of species 1 is maximum where:

$$s_1 = \frac{(a_1a_2 + a_1s_2 - b_1b_2)}{a_2 + s_2} \tag{18}$$

and for species 2 where:

$$s_2 = \frac{(a_1a_2 + a_2s_1 - b_1b_2)}{a_1 + s_1} \tag{19}$$

Combined yield is maximum where:

$$\begin{aligned} s_1 &= \left[\frac{a_1r_2(b_2 - b_1) - b_2r_1(b_1 + b_2) + 2a_1a_2r_1}{4a_1a_2 - (b_1 + b_2)^2} \right] \bullet \left[\frac{a_1a_2 - b_1b_2}{a_2r_1 - b_1r_2} \right] \\ s_2 &= \left[\frac{a_2r_1(b_1 - b_2) - b_1r_2(b_1 + b_2) + 2a_1a_2r_2}{4a_1a_2 - (b_1 + b_2)^2} \right] \bullet \left[\frac{a_1a_2 - b_1b_2}{a_1r_2 - b_2r_1} \right] \end{aligned} \tag{20}$$

THE STOCHASTIC MODEL

The stochastic version of the Lotka-Volterra competition equations has been the subject of some study (see Bartlett, 1960, chapter 5, for a summary). Following the presentation of Leslie & Gower (1958), the continuous time stochastic model may be written:

$$\left.\begin{aligned} \delta N_1 &= (r_1N_1 - a_1N_1^2 - k_1a_1N_1N_2)\,\delta t + \delta Y_1 - \delta Z_1 \\ \delta N_2 &= (r_2N_2 - a_2N_2^2 - k_2a_2N_1N_2)\,\delta t + \delta Y_2 - \delta Z_2 \end{aligned}\right\} \left(k_i = \frac{b_i}{a_i}\right) \tag{21}$$

The quantities δY_i, δZ_i ($i = 1, 2$) are independent, modified Poisson variables with zero means; their variances, when it is assumed that the birth rate of each species b_i' is constant and the death rate d_i variable, are:

$$\begin{aligned} \text{Var}\,(\delta Y_i) &= b_i'N_i\,\delta t \\ \text{Var}\,(\delta Z_i) &= (d_iN_i + a_iN_i^2 + k_ia_iN_1N_2)\,\delta t \end{aligned} \tag{22}$$

In this model, the variances in the region of the stationary state are given by:[5]

$$\sigma_1^2 = \frac{b_1'}{a_1} - k_1\sigma_{12}$$

$$\sigma_2^2 = \frac{b_2'}{a_2} - k_2\sigma_{12}$$

$$(k_1k_2 - 1)\ (a_1L_1 + a_2L_2)\ \sigma_{12} = \frac{a_1k_1L_1b_2'}{a_2} + \frac{a_2k_2L_2b_1'}{a_1} \qquad (23)$$

Similar equations may be written for the case in which the death rate is constant.

For situations in which neither birth rate nor death rate is constant a great variety of stochastic models could be constructed depending on the assumptions about birth and death rate functions (Leslie and Gower, 1958). To achieve verisimilitude with fish populations the assumption of birth rate constant seems most reasonable. However it is worth reiterating that alternative models in which the death rate is assumed constant are available. Passing comment is also warranted on the nature of the assumptions in these stochastic formulations. The order of magnitude of the variability is directly related to the processes envisaged in the deterministic model, and will be accordingly appropriate. Thus in the present model the stochastic variability may be attributed to the operation of random factors in birth and death processes.

It may be seen from equations (23) that changes in L_1 and L_2 occasioned by exploitation will result in changes to σ_1^2, σ_2^2 and σ_{12}, but the direction and order of magnitude of the changes in relation to each other will depend on the values of the parameters a_i, b_i and b_i'.

TABLE I. Variances and covariance for various equilibria associated with exploitation in a continuous time stochastic model of interspecific competition. The value 1 in lines 4 and 5 was substituted for 0.

Exploitation								
Fixed		Proportional						
c_1	c_2	s_1	s_2	L_1	σ_1^2	L_2	σ_2^2	σ_{12}
–	–	–	–	2933	6067	667	2317	–2067
0.2	–	–	–	1868	5867	934	2267	–1867
0.4	–	–	–	800	5599	1200	2199	–1599
0.55	–	–	–	1	5334	1400	2041	–1334
–	0.25	–	–	3600	6450	1	2400	–2399
0.4	0.2	–	–	1335	5850	694	2258	–1853
–	–	.0001	–	1915	3772	923	2120	–1282
–	–	.0001	.0002	2130	3765	620	1622	– 954
–	–	.0002	.0004	1699	2499	542	1069	– 498
–	–	.0003	.0006	1420	1965	475	855	– 322
–	–	.0010	.0020	671	812	247	363	– 59

[5]These equations are modified from their original form. Thus σ_1^2 denotes the variance of N_1 and equals L_1^2 (var u_1) of Leslie and Gower. The birth rate is here denoted by b_i' to distinguish from b_i which is used to represent the coefficient of interaction. In Leslie and Gower b_i denotes birth rate.

For the preceding numerical example (with $b_1' = 1.0$, $b_2' = 0.9$) the variances and covariance show remarkably little variation over a wide range of equilibrium values associated with fixed percentage fishing mortality (Table I). Changes in a_i associated with exploitation in proportion to abundance result in substantial reductions in variance. Thus for lines 6 and 10 of the table, equilibrium values are approximately the same for the two types of exploitation but the variances and covariance are substantially larger for the fixed percentage type. This would be expected considering either the nature of equations (23) or the phenomena represented by the two kinds of exploitation. Departures from mean values will evidently be compensated in exploitation proportional to abundance, resulting in a smaller variability than for fixed percentage exploitation.

Figure 7 shows the order of magnitude of two standard deviations for various equilibria for both types of exploitation.

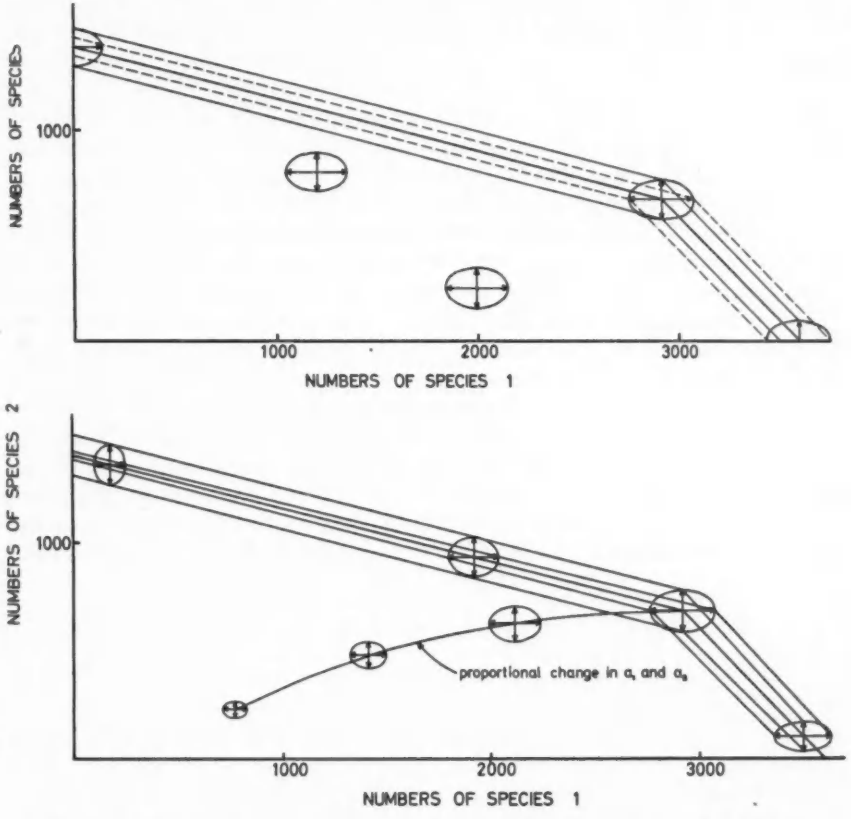

FIG. 7. *Above*: The limits of two standard deviations in the values of N_1 and N_2 in the stochastic model at equilibria related to various rates of fixed-percentage instantaneous fishing mortality. *Below*: The limits of two standard deviations in the values of N_1 and N_2 in the stochastic model at equilibria related to various rates of mortality proportional to abundance.

The stochastic representation of the competitive interaction obviously involves the possibility that a species may be reduced to 0 by chance fluctuation. Assuming that the distributions of $N_1(t)$ and $N_2(t)$ are normal about means for a particular state, the probability of random extinction is given by:

$$P(o) = \frac{1}{\sqrt{2\pi}\sigma_t} e^{-(o-\overline{N}_t)^2/2\sigma_t^2}$$

where the variance σ_t^2 is obtained from equations (23). Very roughly, the mean passage time to extinction is inversely proportional to the probability of the zero state, whence (cf. Leslie & Gower, 1960),

$$\theta_t(o) \sim \sqrt{2\pi}\,\sigma_t\, e^{L_t^2/2\sigma_t^2} \qquad (L_t = \overline{N}_t) \qquad (24)$$

In certain circumstances the mean passage time to extinction approximated by equation (24) may be sufficiently small that it should not be neglected.

Thus, using $\sigma_1 \sim 75$ the mean passage time to extinction for species 1 when $L_1 = 75$ is approximately 300 time units and when $L_1 = 150$ approximately 1400 time units. Similarly, taking $\sigma_2 \sim 50$ mean passage time to extinction for species 2 is approximately 400 where $L_2 = 75$ and 11,000 when $L_2 = 150$. It is thus clear that where exploitation is sufficiently intense to reduce a small population to a very small number of individuals, there is a sizeable probability of random extinction. For a large population, a reduction to a comparable proportion of its original size would not involve a similar risk.

The stochastic model exhibits another feature of interest worthy of mention. The mean equilibrium values, $E\{N_1(t)\}$ and $E\{N_2(t)\}$ are not the same as in the deterministic model. The logistic feature of the population growth processes (i.e., the term $a_t N_t^2$) ensures that a displacement upward from equilibrium will be compensated more than an equal displacement downward. Growing separately, each species would fluctuate around a mean which was less than the deterministic asymptote. When the species are combined in competitive interaction, the means will assume values such that at least one is smaller than in the deterministic model; which one (or both) and to what degree, depending on the relative magnitudes of the r_t, a_t and b_t.[6] In the standard example of this paper, the mean of species 1, under most circumstances of exploitation, is displaced downward proportionately less than that of species 2, and in some instances the mean of species 1 is displaced upward.

EXPLOITATION AND NATURAL REGULATION OF POPULATIONS

The foregoing methods of depicting fixed percentage and "abundance proportional" exploitation may also be considered as depicting respectively the mode of action of density independent and density dependent factors. Thus fixed percentage exploitation is equivalent to the action, on the average, of a density independent mortality factor. Changes in r_t occasioned by the action of some natural factor (climate?, non-specific predator?) would on the average parallel the changes outlined for fixed percentage exploitation. Similarly, a

[6] I am not aware of a mathematical proof of this statement, though it appears to be an obvious feature of the equations.

density-dependent factor (certain types of predator, climatic factors ?) would simulate the proportional exploitation denoted by an increase of s_i on the value a_i. Ostensibly the values b_i represent fixed coefficients of interaction between species, although Dr M. Lloyd has suggested to me that changes in b_i may be taken as simulating modification of habitat, or genetic changes.

If these parallels are accepted the model demonstrates some widely discussed properties of mechanisms of population regulation. Density-dependent factors by definition will not render a population extinct regardless of their intensity, while the same cannot be said of density-independent factors. The addition of a density-dependent factor may preserve an equilibrium that would otherwise not exist. For instance, in the numerical example of the foregoing, if $c_1 = 0.55$ then $N_1 = 0$. If a density-dependent factor of mortality is added which affects both species equally (say $s_1 = s_2 = 0.00025$) then for $c_1 = 0.55$ the system is stable at $N_1 = 255$, $N_2 = 891$. The addition of a density dependent factor affecting both species equally, "preserves" species 1 from extinction. Figure 8,

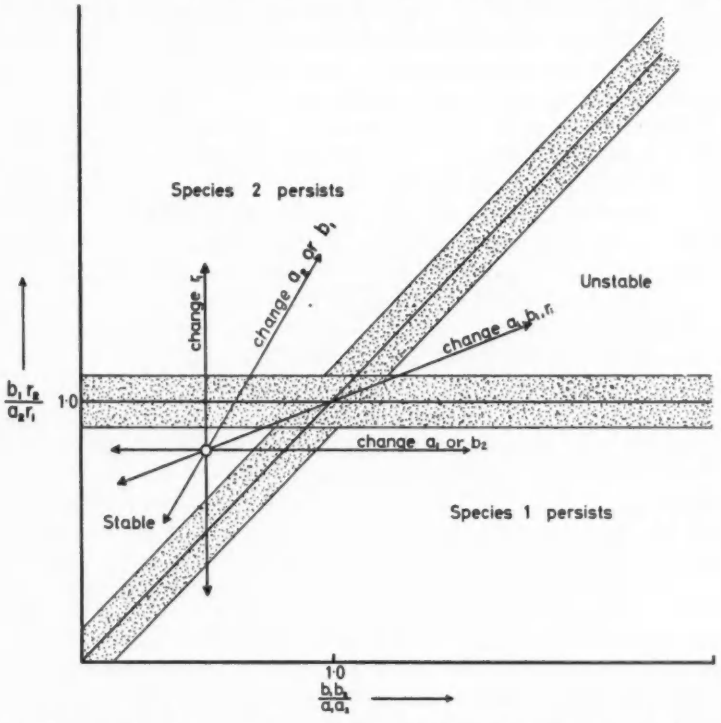

FIG. 8. The effects, on a stable equilibrium, of changes in the parameters of the Lotka-Volterra competition equation. Fixed-percentage instantaneous mortality produces vertical displacement; mortality of species in proportion to abundance produces horizontal displacement; change in coefficients of interactions and/or simultaneous changes in both fixed-percentage and abundance-proportional mortality produce various diagonal displacements. The shaded area schematically denotes where stochastic variability may measurably influence the result.

which is based on a suggestion of Dr P. H. Leslie, illustrates the many similar corollaries which may be drawn. Changes in r_t will displace equilibrium vertically, changes in a_1 or b_2 will displace equilibrium horizontally, changes in a_2 or b_1 displace equilibrium along the vector through the origin, and changes in combinations of a_t, b_t and r_t simultaneously, displace equilibrium between wide limits that may include the unstable state. The shaded boundaries are a schematic representation of the zone in which stochastic variability may contribute measurably to the outcome.

Laboratory examples of these kind of phenomena are available in the work of Gause (1935) and Slobodkin (1960) and many others. In his dilution experiments, Gause in effect sustained an equilibrium by "harvesting" the same fixed percentage of two competing species of *Paramoecium*. Slobodkin maintained cultures of green and brown hydra by raising the animals in the dark (habitat change) or by removing a fixed percentage of newborn animals. Utida (1953) maintained two competing species of weevil by the introduction of a parasitic wasp. It is not suggested that these experimental studies are explained by the model here presented; rather only that the *kinds* of phenomena the model depicts have been observed in some studies.

Depicting the action of natural factors as types of exploitation in a model raises the problem of how to represent the variability in their intensity. For the effect on reproduction of density-independent factors Ricker (1954) argued that a "normal frequency distribution provides a fairly realistic picture of the relative frequencies of the resultants of the various independent factors making for success or failure in reproduction". However, he pointed out, their effect on reproductive potential is multiplicative rather than additive. Accordingly, he chose a log normal distribution for depicting effects of variation of density-independent factors on success of reproduction. Applying this reasoning to the present model, it is clear that adding a fixed percentage density-independent factor m_t as an *instantaneous* rate associates arithmetic fluctuation in m_t with logarithmic fluctuation in "reproduction". For example, if $\lambda_t = e^{r_t - m_t}$ then arithmetic change in m_t is associated with logarithmic change in λ_t. (However there is the important difference that various intensities of effect are no longer represented as varying proportions of the *average*, but rather as varying proportions of the theoretical 'maximum rate.) The question of the type of frequency distribution involved is less straightforward. Ricker argues that "extremes of environmental conditions are less common than conditions approaching normal". While this may be true of an imaginary totality of density-independent effects it may not apply to the incidence of a particular factor.

In the sections following, density-independent factors were arbitrarily visualized as having a uniform random distribution over a specified range which was some multiple of the death rate. Symbolically, equations (1) in this instance would take the form:

$$\frac{dN_1}{dt} = (b_1' - d_1)\, N_1 - R_1 Q_1 d_1 N_1 - a_1 N_1^2 - b_1 N_1 N_2$$

$$\frac{dN_2}{dt} = (b_2' - d_2)\, N_2 - R_2 Q_2 d_2 N_2 - a_2 N_2^2 - b_2 N_1 N_2 \qquad (25)$$

where R_1 and R_2 are random numbers of range 0 to 1, and Q_1 and Q_2 are coefficients specifying the magnitude of effect. Since Q_1 may not be equal to Q_2 this formulation provides for the possibility that the two competitors may be affected differentially by climatic factors. A further avenue of exploration is suggested by setting $R_1(t)$ equal to $R_2(t)$, in which case the two competitors would be exposed to the same random sequences (perhaps simulating common susceptibility to a particular environmental factor).

Variability in density-dependent factors is related to the kind of mechanism envisaged. The stochastic model of population growth (or the foregoing stochastic model of competitive interaction) incorporates density-dependent processes. Similarly a three-species system of two competitors and a predator would have an intrinsic variability which was a function of the birth and death rates and the modes of interactions. This type of system has not been explored theoretically and poses difficult problems of representation. However, there is one particular kind of density-dependent factor which can easily be incorporated in the foregoing competition model. Several workers, notably Andrewartha and Birch (1954) have argued that climate may remove animals in a density-dependent way. The distinction must be made that while this type of climatic factor may affect a proportion of the population which depends on density, it may not necessarily act at the appropriate time to "regulate" the population. In essence, climatic density-dependent factors have a variability which is extrinsic to the biological system they influence. This type of influence can be incorporated in the model in a similar way to that used for density-independent factors. Equations (1) will then take the form:

$$\frac{dN_1}{dt} = r_1N_1 - (a_1N_1^2 + S_1P_1a_1N_1^2) - b_1N_1N_2$$

$$\frac{dN_2}{dt} = r_2N_2 - (a_1N_2^2 + S_2P_2a_2N_2^2) - b_2N_1N_2 \qquad (26)$$

where S_1 and S_2 are random numbers of range 0 to 1, and P_1 and P_2 are coefficients specifying the magnitude of the effect in relation to a_1 and a_2 respectively. Both the order of magnitude and the random sequences can be made the same or different.

It should be emphasized that this formulation depicts a density-dependent factor for which the variability is extrinsic of the system being influenced. It is intended primarily to simulate climatic density-dependent factors, although it is possible that there may be some biological counterparts.

THE DISCRETE TIME MODEL

For the description of transitions from one steady state to another, and for study of extinction probabilities it is convenient to deal with a discrete time model using a computer for laborious calculations. Following Leslie (1958) and Leslie and Gower (1958), a discrete time model for equations (1) is:

$$N_1(t+1) = \frac{\lambda_1N_1(t)}{1 + \alpha_1N_1(t) + \beta_1N_2(t)}$$

$$N_2(t+1) = \frac{\lambda_2N_2(t)}{1 + \alpha_2N_2(t) + \beta_2N_1(t)} \qquad (27)$$

The relations between the constants and those of the continuous time model are:

$$\begin{aligned} \lambda_i &= e^{r_i} \\ \alpha_i &= \frac{\lambda_i - 1}{K_i} \\ K_i &= \frac{r_i}{a_i} \\ \beta_i &= \frac{\alpha_i b_i}{a_i} \end{aligned} \tag{28}$$

Introducing exploitation into a stable equilibrium to parallel the deterministic model can be achieved by setting:

$$\begin{aligned} \lambda_i' &= e^{r_i'} \\ \alpha_i' &= \frac{\lambda_i' - 1}{K_i'} \\ K_i' &= \frac{r_i'}{a_i} \\ \beta_i' &= \frac{\alpha_i' b_i}{a_i} \end{aligned} \tag{29}$$

This procedure is not immediately evident and at first sight suggests that in calculating the new values α_i' and β_i' the basic parameters of the competitive system are being altered. However, bearing in mind that the simulation of the discrete time model depends on preserving the interrelationship between r_i, a_i and b_i when substituting $\lambda_i - 1$, α_i and β_i, the procedure is straightforward.

Equilibrium in the discrete time model is given by:

$$\begin{aligned} N_1 = L_1 &= \frac{\alpha_2(\lambda_1 - 1) - \beta_1(\lambda_2 - 1)}{\alpha_1\alpha_2 - \beta_1\beta_2} \\ N_2 = L_2 &= \frac{\alpha_1(\lambda_2 - 1) - \beta_2(\lambda_1 - 1)}{\alpha_1\alpha_2 - \beta_1\beta_2} \end{aligned} \tag{30}$$

Yield can be expressed in two ways in a discrete time system, depending on whether cropping takes place within or only at the termination of each time period. If the instantaneous mortality rate e^{-c_i} is applied during the time period t to $t + 1$ as is implied in equations (29) then the yield is the same as in the continuous time model and is given by $c_i N_i(t)$ (see Fig. 2–5). However, it may be visualized that the cropping mortality and the natural birth and death processes may not be distributed proportionately during the time period. For instance, the cropping mortality may occur at the end of the time period, after the natural processes are completed. In this instance yield for species 1, say, will be given by:

$$Y_1 = \frac{\lambda_1 N_1(t)}{1 + \alpha_1 N_1(t) + \beta_1 N_2(t)} - N_1(t) \tag{31}$$

For the estimation of maxima this kind of implicit difference equation is intractable. However, it is clear that this quantity will always be less for the

same equilibria than the continuous time model. Figure 9 gives yield isopleths based on individual calculations for various equilibria for the previous example. The basic parameters were:

$$\lambda_1 = 2.4596 \qquad \alpha_1 = 0.0004054 \qquad \beta_1 = 0.0004054$$
$$\lambda_2 = 2.0138 \qquad \alpha_2 = 0.0007241 \qquad \beta_2 = 0.000181025$$

At all equilibria the yields are lower than for the uniformly distributed instantaneous mortality of the continuous time model (or its discrete time counterpart) as shown in Fig. 4. The point of maximum combined yield lies close to the equilibrium $N_1 = 1387$, $N_2 = 25$, compared to $N_1 = 1774$, $N_2 = 35$ in the continuous time version. The general form of the isopleths reflects the shift of the point of maximum yield, otherwise the pattern is similar.

The stochastic version of the discrete time model (Leslie, 1960) estimates the variance of the expected $N(t+1)$ as:

$$\sigma^2\{N(t+1) \mid N(t)\} = \phi_t E\{N(t+1) \mid N(t)\} \tag{31A}$$

Equations (27) may be rewritten in the form:

$$N(t+1) = \lambda_t N(t)$$

where for species 1, say:

$$\lambda_1(t) = \frac{\lambda_1}{1 + \alpha_1 N_1(t) + \beta_1 N_2(t)}$$

Then, when the birth rate is constant:

$$\log_e \lambda_t = r_t = b' - d_t$$
$$\phi_t = \left(\frac{2b'}{r_t} - 1\right)(\lambda_t - 1) \quad (\lambda_t \neq 1)$$
$$= 2b' \quad (\lambda_t = 1) \tag{32}$$

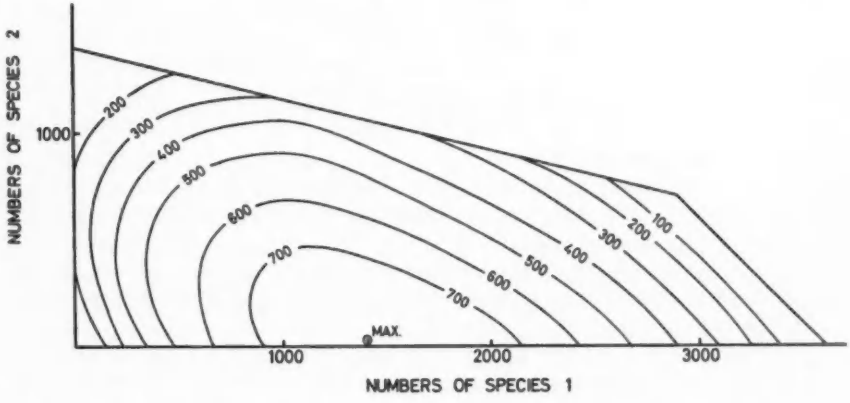

FIG. 9. Combined sustained yield of species 1 and species 2 at various equilibria in the discrete time model when it is assumed that cropping occurs at the end of each time period. The maximum is near $N_1 = 1387$, $N_2 = 25$.

The variance in a discrete time model is always greater than in the continuous time equivalent, although the discrepancy can be made small by reducing the unit of time adopted in the discrete time model. (Bartlett *et al.*, 1960). Provided that $\lambda \leq 2$ and $b' \leq 1$ (Leslie, 1960), the value ϕ_t is approximately given by:

$$\phi_t \sim (b' + 1) + (b' - 1)\,\lambda_t \tag{33}$$

Variance in the region of the stationary state in the discrete time model can be estimated from the theory of small fluctuations (Leslie & Gower, 1958). Equation (27) may be written, for species 1, as:

$$f_1 = \frac{\lambda_1 N_1}{1 + \alpha_1 N_1 + \beta_1 N_2}$$

We have then:

$$\left(\frac{df_1}{dN_1}\right)_{L_1L_2} = 1 - \frac{\alpha_1 L_1}{\lambda_1}, \left(\frac{df_1}{dN_2}\right)_{L_1L_2} = -\frac{\beta_1 L_1}{\lambda_1}$$

Similarly, for species 2 we may write:

$$\left(\frac{df_2}{dN_2}\right)_{L_1L_2} = 1 - \frac{\alpha_2 L_2}{\lambda_2}, \left(\frac{df_2}{dN_1}\right)_{L_1L_2} = -\frac{\beta_2 L_2}{\lambda_2}$$

Denoting these four derivatives as x_1, x_2, y_1 and y_2 respectively, the set of equations for determining the variances and the covariance of N_1 and N_2 are:

$$\begin{aligned} \sigma_1^2 &= (x_1)^2\sigma_1^2 + 2(x_1x_2)\ \mathrm{cov} + (x_2)^2\sigma_2^2 + \sigma^2(Z_1) \\ \sigma_2^2 &= (y_2)^2\sigma_1^2 + 2(y_1y_2)\ \mathrm{cov} + (y_1)^2\sigma_2^2 + \sigma^2(Z_2) \\ \mathrm{cov} &= (x_1y_2)\ \sigma_1^2 + (x_1y_1 + x_2y_2)\ \mathrm{cov} + (x_2y_1)\ \sigma_2^2 \end{aligned} \tag{34}$$

where $\sigma^2(z_i) \sim 2N_i(t + 1)$ at the stationary state at which $\lambda(t) \sim 1$.

COMPUTER PROGRAMMING

The discrete time stochastic model was programmed in "Manchester Mercury Autocode" and machine calculations were performed at the Oxford University Computing Centre. Following the technique of Leslie and Gower (1958), random normal deviates for stochastic variability were obtained by summing 12 random variates (uniform in the range $-\frac{1}{2} \leq x \leq \frac{1}{2}$) which were generated in the "Autocode" random number subroutine. The program was designed to provide for any one,or any combination of the following alternatives:

1. Deterministic or stochastic
2. Fixed percentage and/or proportional exploitation
3. Randomly variable density-independent and/or randomly variable density-dependent mortality
4. Each of effects No. 3 of same or different magnitude for the two species
5. Each of effects No. 3 on the same or different random sequences for the two species.

At the end of each time period $N(t)$ was rounded to the nearest integer. In most instances the process was terminated at 100 time periods. The stochastic variance was in all instances estimated by equation (33) a procedure which was in most instances satisfactory, because about equilibria the value $\lambda(t) \sim 1$ and under a wide variety of exploitation rates $\lambda_t \leq 2$.

Transition Sequences and Yield

Typical transition sequences of N_1 and N_2 to new exploitation equilibria are shown in Fig. 10. After an initial displacement of the exploited species in the first time period, the relation between the two species gradually proceeds asymptotically in the direction of the new equilibrium. As expected, the transition to a new equilibrium is more rapid when the exploitation is proportional to abundance. If no convention is adopted about the significance of fractions of animals, the process takes an infinite time; for instance, there is always some minute fractional residue of a species destined for extinction. When the number of each species is rounded to the nearest integer, at the end of each time period, the process comes to a halt when the complementary effects of the competitors on each other will not cause a change greater than one half an individual during one time period. In consequence, in the familiar example on which Fig. 10 is based, the attempt to eliminate species 1 by a fixed fishing

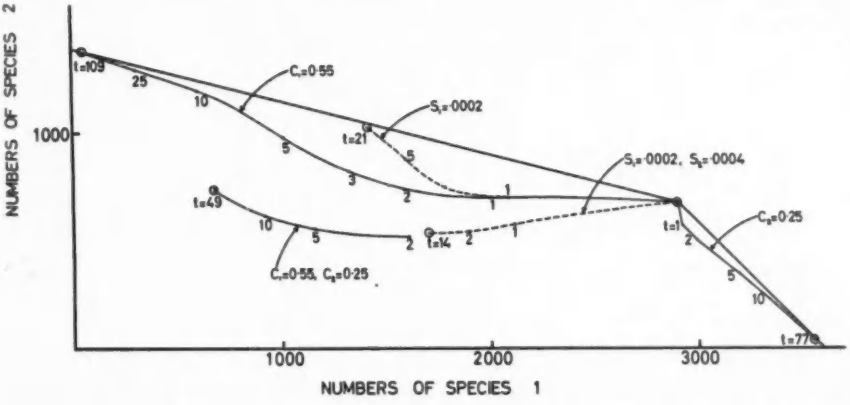

FIG. 10. Transition sequence in deterministic discrete time model from original equilibrium to various exploitation equilibria. The terminal points are rounding end points that fall short of the theoretical equilibria. Numbers refer to time periods required.

mortality rate of $c_1 = 0.55$ culminates in $N_2 = 1386$, $N_1 = 56$ at $t = 109$, rather than at the theoretical end point of $N_1 = 0$, $N_2 = 1400$ at $t = \infty$. Similarly, the attempt to eliminate species 2 by a fixed fishing mortality rate of $c_2 = 0.25$ terminates at $N_1 = 3560$, $N_2 = 40$ at $t = 77$, rather than at $N_1 = 3600$, $N_2 = 0$ at $t = \infty$. The same is true for exploitation proportional to abundance, though from the nature of the equations, the rounding end point is closer to the theoretical equilibrium. Where $s_1 = 0.00040$, theoretical equilibrium is at $N_1 = 3277$, $N_2 = 323$, but with rounding, the discrete time model terminates at $N_1 = 3275$, $N_2 = 325$ at $t = 24$. For $s_1 = 0.0002$, $s_2 = 0.0004$, the end point is $N_1 = 1700$, $N_2 = 541$ at $t = 14$, rather than $N_1 = 1700$, $N_2 = 54$ at $t = \infty$.

The stochastic process involves the same rounding procedure. However, transition to any particular state, including extinction, is a possibility, which will

transpire in a passage time that depends both on the initial number (in this case those of the original pre-exploitation equilibrium) and the parameters for interaction of the competitors. For instance, when species 2 is exploited at $c_2 = 0.25$ extinction usually occurs in the stochastic model before $t = 100$ (Table II), although in the deterministic model the rounding end point, where $N_2 = 40$, is reached at $t = 77$. It is perhaps an important feature of the stochastic model, that dealing in whole animals (which is realistic) does not involve the nuisance of a rounding end point.

TABLE II. Computed outcomes for each of 10 replicates of various kinds and degrees of exploitation in stochastic competition models. For each series of replicates the random normal variate sequence had the same starting point.

Fixed Percentage Exploitation

$c_1 = 0.55$			$c_2 = 0.25$			$c_1 = 0.55$	$c_2 = 0.25$	
Time periods	Final N_1	Final N_2	Time periods	Final N_1	Final N_2	Time periods	Final N_1	Final N_2
100	224	1290	44	3590	0	100	861	639
100	99	1196	69	3505	0	100	738	584
94	0	1293	76	3901	0	100	629	657
100	26	1405	67	3648	0	100	531	873
100	115	1455	90	3648	0	100	789	723
100	26	1439	100	3527	37	100	636	705
100	167	1378	100	3761	8	100	743	684
100	48	1476	79	3703	0	100	626	862
100	61	1322	80	3652	0	100	497	679
100	43	1363	66	3633	0	100	658	777
Theoretical end point	0	1400		3600	0		667	733
Deterministic rounding end point	56	1384		3560	40		672	731

Exploitation Proportional to Abundance

$s_1 = 0.0002$			$s_2 = 0.0004$			$s_1 = 0.0002$	$s_2 = 0.0004$	
100	1582	960	100	3493	264	100	1854	482
100	1457	875	100	3311	229	100	1727	422
100	1346	962	100	3184	251	100	1612	481
100	1343	1165	100	3153	423	100	1633	627
100	1497	1051	100	3375	328	100	1774	547
100	1387	1005	100	3233	303	100	1668	513
100	1392	1017	100	3220	297	100	1652	525
100	1384	1183	100	3226	419	100	1673	641
100	1290	984	100	3133	276	100	1579	492
100	1432	1081	100	3295	355	100	1718	569
Theoretical end point	1419	1045		3277	323		1700	543
Deterministic rounding end point	1421	1044		3275	325		1700	541

Table II summarizes the computer output for 6 exploitation procedures in the standard example. For each series of 10 replicates the random normal deviate sequence had the same starting point. The time required to reach a deterministic end point is lower in exploitation proportional to abundance, reflecting its density-dependent effect. In each instance where extinction is not involved there is no significant difference between the theoretical end point and the mean of the stochastic end points at $t = 100$.

A typical transition sequence for fixed percentage exploitation in the stochastic model, the first replicate where $c_1 = 0.55$, $c_2 = 0.25$ in Table II, is shown in Fig. 11. It is difficult to say exactly when the process has reached an equilibrium, but by $t = 20$, the values of N_1 and N_2 were usually well within the range of fluctuation from $t = 20$ to $t = 100$.

For this series of time periods for the first 3 replicates the variances and means compared to those for the theoretical continuous time and discrete time model were:

			Theoretical	
	Empirical		Continuous time	Discrete time
σ_1^2	4651.6	(1)		
	4206.9	(2)	5666.7	7267.7
	7915.4	(3)		
σ_2^2	2654.5	(1)		
	2357.8	(2)	2216.7	3369.9
	1830.5	(3)		
σ_{12}	+ 277.2	(1)		
	+ 127.9	(2)	− 1666.7	− 2070.4
	− 214.2	(3)		
N_1 (mean)	724.9	(1)		
	707.7	(2)	666.7	
	681.9	(3)		
N_2 (mean)	692.4	(1)		
	718.1	(2)	733.3	
	697.3	(3)		

The agreement between theoretical and empirical values is fair, especially considering the sample sizes. The discrepancy in the co-variances is large and consistent and no simple explanation seems available (unless the assumption that equilibrium is reached by $t = 20$ is invalid).

Observing that the yield in this situation would be given in each time period by $c_i N_i(t)$, yields can be calculated under the condition of the fixed rate of instantaneous fishing mortality for each species. Figure 12 shows the fluctuation in yield of each species, and for both combined, from $t = 20$ to $t = 90$ in the first replicate of the foregoing example. The variations in yield are substantial,

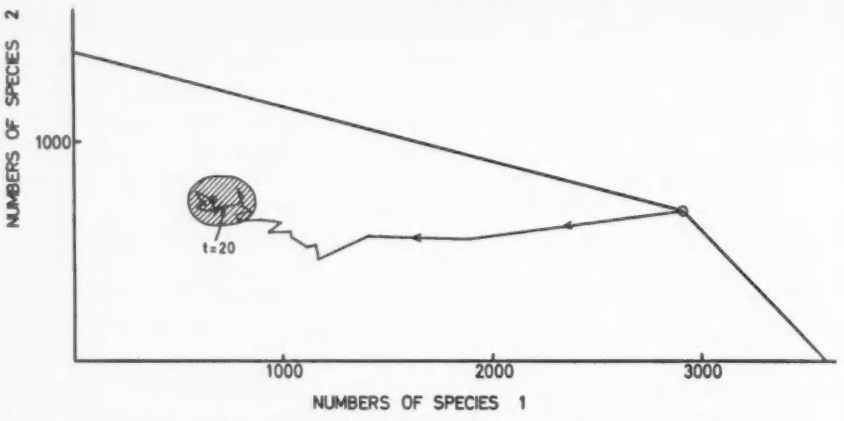

FIG. 11. Transition sequence from $t = 0$ to $t = 31$ in stochastic discrete time model from original equilibrium to $N_1 = 667$, $N_2 = 733$ as a result of exploitation at $c_1 = 0.55$, $c_2 = 0.25$. Shaded elliptical area indicates region of fluctuation from $t = 20$ to $t = 100$.

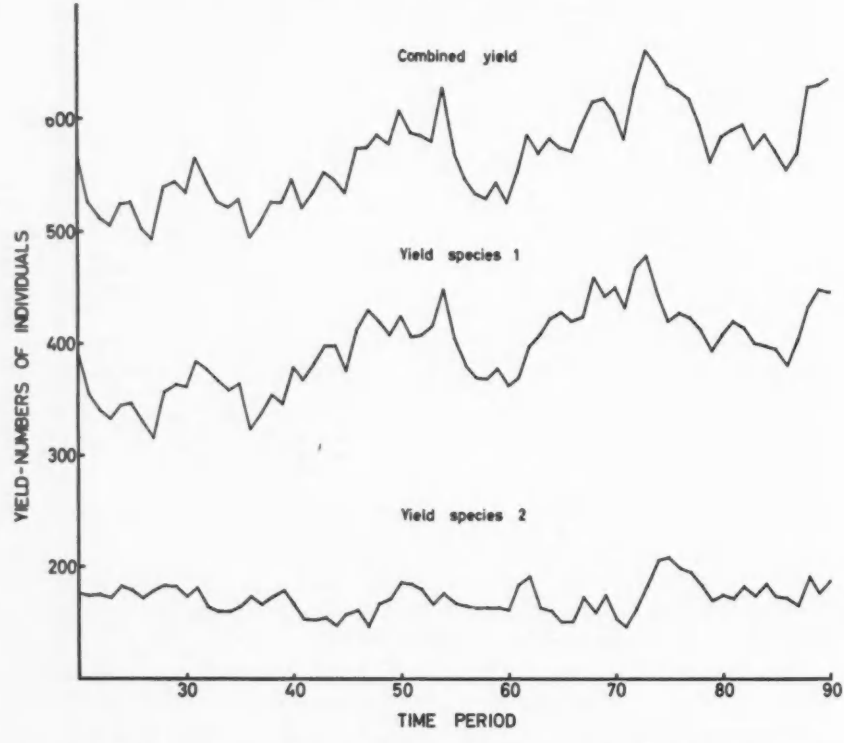

FIG. 12. Yield from fixed-percentage fishing mortality in the stochastic discrete time model from $t = 20$ to $t = 100$, in the example of Fig. 11 where $c_1 = 0.55$, $c_2 = 0.25$.

and underline the role stochastic processes may play in population dynamics. To take a single instance, between $t = 54$ and $t = 60$ the yield of species 1 declined from 447 to 361 individuals, a result entirely the consequence of chance elements in the birth and death processes. Fluctuations of this order of magnitude relative to population size would not occur in large populations.

Fluctuations about an exploitation equilibrium are theoretically smaller for exploitation proportional to abundance and are also shown in the computer runs. For instance, in the first replicate in Table II where $s_1 = 0.0002$, $s_2 = 0.0004$, the random normal deviate sequence was the same as for the example of fixed percentage exploitation just discussed ($c_1 = 0.55$, $c_2 = 0.25$). The process reached the exploited equilibrium by $t = 12$.

For the time period $t = 20$ to $t = 100$ the variances compared to those for the theoretical continuous time and discrete time models were:

		Theoretical	
	Empirical	Continuous time	Discrete time
σ_1^2	4190.5	2498.8	4611.9
σ_2^2	2039.1	1069.1	1936.3
σ_{12}	− 255.75	− 497.8	− 399.7
N_1 (mean)	1721.4	1700	
N_2 (mean)	519.4	543	

The agreement between the observed and theoretical variances seems quite satisfactory in this instance.

"Yield" with exploitation proportional to abundance is given by $s_i N_i^2(t)$ and represents the number of animals removed in each time period (see Fig. 13 for example just cited). Short term fluctuations in yield are more marked than in fixed percentage exploitation (Fig. 12) despite the smaller variances of population sizes; a paradox consistent with the compensatory aspect of exploitation proportional to abundance.

Effects of Extrinsic Factors

A great many different kinds and combinations of extrinsic effects could easily be studied using the computer program. However, the results obtained have no inherent interest except as they provide some basis for generalization other than that available from a purely algebraic treatment. The conclusions regarding the way in which changes to r_i, a_i and b_i may influence the result of a competitive interaction, as summarized in Fig. 8 can readily be confirmed in the stochastic discrete time model.

The addition of a density-independent factor of mortality (with uniform random variation) accelerates extinction when applied equally to both an exploited species and its competitor. Applying a differential mortality, less severe to the exploited species, may delay extinction but only where the effect of increased mortality to the exploited species is more than offset by the differential mortality to its competitor. For instance, where $c_1 = 0.55$, $c_2 = 0$, the addition

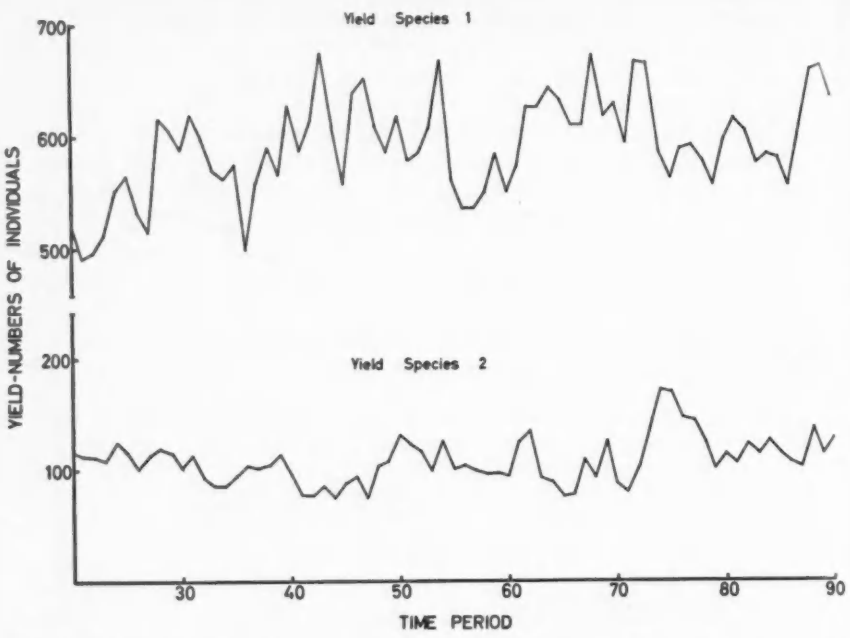

FIG. 13. Yield from exploitation proportional to abundance in the stochastic discrete time model from $t = 20$ to $t = 100$, where $s_1 = 0.0002$, $s_2 = 0.0004$.

of a density-independent mortality of mean 0.1 to species 1 and mean 0.2 to species 2, has no measurable effect by $t = 100$ in delaying the decline of species 1 to extinction. The average abundance of the two species at $t = 100$ in 10 replicates of this situation was $N_1 = 54$, $N_2 = 702$ compared to $N_1 = 81$, $N_2 = 1362$ where no additional mortality factor was involved (Table II, $c_1 = 0.55$).

In the situation where $c_1 = 0.55$ and species 1 should be eliminated, the addition of a factor which acts in a density-dependent manner, but with a severity which fluctuates randomly in time, will preserve species 1 indefinitely. Table III gives 4 sets of computer results for this kind of situation. For the first 2 sets, the species were affected by different sequences of random numbers which were scaled on the average, to make α_1' twice as large. In the first set α_2 was also made twice as large; in the second α_2 was made 1.5 times as large. In both instances the numbers of species 1 at $t = 100$ were substantially above extinction levels and in the vicinity of the theoretical deterministic equilibria.

An interesting feature is provided by comparison of sets 1 and 2 with sets 3 and 4 respectively in Table III. The latter were computed with both species influenced by the *same* sequence of random density-dependent effects. Surprisingly, the results appear identical to those for the first two sets in which a different sequence of random numbers was used for each species. The same phenomenon was observed in computer runs for density-independent factors of

TABLE III. Numbers of species 1 and species 2 after 100 time periods where $c_1 = 0.55$, but species 1 is not eliminated because of the addition to α_i of a density-dependent mortality factor which affects both species in a random sequence with mean $R_i\alpha_i$. ($\alpha_1' = 0.000299357$, $\alpha_2 = 0.0007241$).

Different random number sequence				Same random number sequence			
Set 1		Set 2		Set 3		Set 4	
$R_1 = R_2 = 1$		$R_1 = 1$	$R_2 = 0.5$	$R_1 = R_2 = 1$		$R_1 = 1$	$R_2 = 0.5$
N_1	N_2	N_1	N_2	N_1	N_2	N_1	N_2
251	843	156	1056	275	770	170	997
317	806	106	1040	279	859	79	1084
387	814	163	1050	333	973	165	1160
349	974	222	1165	335	1042	211	1213
388	939	270	1115	407	842	274	1047
304	916	158	1117	324	1013	170	1186
267	930	148	1127	282	1053	156	1214
487	1019	372	1159	504	859	374	1051
310	988	178	1188	351	847	197	1080
354	768	208	978	342	802	195	1006
Mean 341.4	899.7	198.1	1099.5	343.2	906.0	199.1	1103.8
Deterministic Mean 350.0	875.0	215.4	1076.9	350.0	875.0	215.4	1076.9
Variance 4706.0	7440.2	5787.7	4401.2	4783.1	10816.7	6166.8	6880.8

mortality. The inference would seem to be that if the competitors are influenced by the same density-dependent or density-independent climatic factors the ultimate result is the same as if they were affected by quite different factors (both sets being randomly selected).

DISCUSSION

From the Lotka-Volterra formulation of competitive interaction it can be deduced that with exploitation of either or both of two competing species in a stable stationary state the equilibrium population sizes will be shifted. With sufficiently intense fixed percentage exploitation one species may be eliminated. Yield of either species is greater in any set of conditions when its competitor is also harvested, in consequence of which there are opportunities for making misleading stock assessments if the effect of competition is not appreciated. Exploitation in proportion to abundance will not render a species extinct, and shifts to new equilibria are more rapid than for fixed percentage exploitation.

These properties of the Lotka-Volterra system may have significant application to applied fisheries biology. It is unlikely that opportunities will commonly be provided for studying the competitors both as separate populations and as an interacting system. In consequence, evaluation of the 6 parameters for fitting the equations to field conditions would seem to require measurement of yield under at least 5 steady states of exploitation. Alternatively, the parameters of the discrete time model can be estimated using serial correlation tech-

niques, provided there are sufficient observations of population size about a single steady state. However, in both instances fluctuations in population size related to year-class success, and all the other inherent difficulties of achieving steady state conditions in natural stocks under exploitation, would seem to militate against precise application of the model to a field situation. Nevertheless, the conclusions derived from the theoretical treatment have suggested profitable lines for experimental manipulation of stocks, and provide some basis for explanation of the failure of populations to respond in conformity with a single species model.

The observations of Omand (1951) reflect awareness of the consequences of interspecific competition in exploitation, and provide examples of some of the factors which might complicate field analysis. For instance, smallmouth black bass (*Micropterus dolomieu*) and bullheads (*Ameiurus nebulosus*) are affected by the same fishing effort, and may occupy the same environment at the time of year when fishing is conducted. However, fishing effort on smallmouth bass does not (at least in the short term) substantially reduce populations of sunfish (*Lepomus gibbosus*) or rock bass (*Ambloplites rupestris*); apparently because these latter species are either confined to different habitats in the fishing season or are more active in dispersing to depleted areas.

In its stochastic version, the model seems particularly suited for study of small natural populations of competitors exposed to "exploitation" by either artificial (man made) or natural agencies. A mixed species population of competitors may owe its stability to the action of factors of mortality extrinsic to the interacting system. Conversely, the addition of new factors of mortality may eliminate one of the species in an otherwise stable association. In these situations, stochastic variability makes random extinction a possibility to which can be attached a quantitative measure of likelihood. It may be envisaged that a species population is subdivided into a number of spatially separate and small "cells of interaction" (Gause, 1934; Nicholson, 1933; Huffaker, 1958; Andrewartha and Birch, 1954). In this situation, the stochastic process may have a significant role with dispersal in shaping the nature of the mechanics of changes in large populations. For example, one may consider populations of large mammals (say mountain sheep) or small populations of pond fishes, that persist as small colonies in refuges between which immigration is negligible. Each colony, being small, may have a sizeable probability of random extinction, which may be augmented by competition particularly if differential exploitation is involved. In time, each of these colonies would become extinct. Without immigration, the whole species population would eventually disappear, having fallen victim to the combined effects of subdivision, competition and exploitation.

The discrete time model can be constructed so that the properties of the system can be simulated and studied by computer. In addition to the therapy that a computer provides for the algebra of a biologist, it can be used for empirical assessment of a variety of specific effects which may have particular interest but are difficult to handle theoretically. A case in point is the observation that there was no apparent difference when competitors were exposed to the same or

different random sequences of environmental effects having the same average intensity.

In some respects the Lotka-Volterra formulation may seem inadequate as a representation of natural situations. For instance it requires that there be an instantaneous response in the interaction between the species, when in fact a substantial time lag should be incorporated. Depending on the kind of time lag envisaged (Wangersky and Cunningham, 1957) appropriate changes can be made in the model and in computer programs for their study. Similarly, a simulation of a "refuge" of a few specialized niches for either or both species can be incorporated in the model.

More serious is the fact that, as it stands, the model provides no recognition, *per se*, of age-class structure nor of some other vital statistics which may be pertinent. Where such considerations refute the broad associative depiction of the Lotka-Volterra equations, alternative models are certainly desirable. However, the deterministic versions of age-class models which consider separate age-class interactions, pose formidable problems in the solution of autonomous equations. Stochastic versions of age-class models at present seem difficult if not impossible of solution (Bharucha-Reid, 1960, p. 187). Accordingly, it may be necessary to sacrifice some verisimilitude in the interests of making approximations of the general consequences of certain kinds of interactions.

It seems appropriate to conclude that this formulation of competition and exploitation together with variations should now be applied to a laboratory or natural situation to test its usefulness as a basis for prediction.

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REFERENCES

ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. Univ. Chicago Press. 782 pp.

BARTLETT, M. S. 1960. Stochastic population models in ecology and epidemiology. *Methuen Monogrs. Appl. Prob. and Stat.* London. 90 pp.

BARTLETT, M. S., J. C. GOWER AND P. H. LESLIE. 1960. A comparison of theoretical and empirical results for some stochastic population models. *Biometrika*, **47**: 1–11.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. *U.K. Ministry Agric., Fish. and Food, Fishery Invest.*, Ser. II, **19**: 533 pp.

BRIAN, M. V. 1956. Exploitation and interference in interspecies competition. *J. Animal Ecol.*, **25**: 339–347.

D'ANCONA, U. 1942. La lotta per l'esistenza. Giulio Einaudi, Torino, Italy.

GAUSE, G. F. 1935. Vérifications expérimentales de la théorie mathématique de la lutte pour la vie. *Actualités Sci. et Indust.*, No. 270, 61 pp., Hermann, Paris.

GRAHAM, MICHAEL. 1939. The sigmoid curve and the overfishing problem. *Cons. Perm. Internat. pour l'Explor. de la Mer, Rapp. et Proc.-Verb.*, **110**: 17–20.

HUFFAKER, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, **27**(14): 343–383.

JOHANNES, R. E., AND P. A. LARKIN. 1960. Competition for food between redside shiners (*Richardsonius balteatus*) and rainbow trout (*Salmo gairdneri*) in two British Columbia Lakes. *J. Fish. Res. Bd. Canada*, **18**(2): 203–220.

LARKIN, P. A. 1956. Interspecific competition and population control in freshwater fish. *J. Fish. Res. Bd. Canada*, **13**(3): 327–342.

LESLIE, P. H. 1958. A stochastic model for studying the properties of certain biological systems by numerical methods. *Biometrika*, **45**: 16–31.

1960. A note on some approximations to the variance in discrete-time stochastic models for biological systems. *Ibid.*, **47**: 196–197.

1962. A stochastic model for two competing species of *Tribolium*, and its application to some experimental data. *Ibid.*, **49**: 1–25.

LESLIE, P. H., AND J. C. GOWER. 1958. The properties of a stochastic model for two competing species. *Biometrika*, **45**: 316–330.

1960. The properties of a stochastic model for the predator-prey type of interaction between two species. *Ibid.*, **47**: 219–234.

NICHOLSON, A. J. 1933. The balance of animal populations. *J. Animal Ecol.*, **2**(1): 132–178.

OMAND, D. N. 1951. A study of populations of fish based on catch-effort statistics. *J. Wildlife Management*, **15**(1): 188–198.

RICKER, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Canada*, **11**(5): 559–623.

1958a. Maximum sustained yields from fluctuating environments and mixed stocks. *Ibid.*, **15**(5): 991–1006.

1958b. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

SHORYGIN, A. A. 1946. Seasonal dynamics of food competition of fishes. *Zool. Zhurnal*, **25**(5): 441–450. (Cited from Beverton and Holt, 1957).

SLOBODKIN, L. B. 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York, 184 pp.

UTIDA, SYUNRO. 1953. Interspecific competition between two species of bean weevil. *Ecology*, **34**(2): 301–307.

WANGERSKY, P. J., AND W. J. CUNNINGHAM. 1957. Time lag in population models. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**: 329–338.

Marine Fish Tissue Culture[1]

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ABSTRACT

Cell proliferation of tissue explants of different organs from marine fish has been achieved in a nutrient solution composed of Medium 199 plus 10% human serum. Fin, spleen, heart, kidney, liver, gonad, brain, uterus, and thymus tissues have been cultured. The tissues were obtained from sexually mature Atlantic cod (*Gadus morhua*), white perch (*Roccus americanus*) winter flounder (*Pseudopleuronectes americanus*), thorny skate (*Raja radiata*), American goosefish (*Lophius americanus*), pollock (*Pollachius virens*), and shorthorn sculpin (*Myoxocephalus scorpius*). An actively dividing cell culture of flounder kidney cells prepared by mechanical disruption of the kidney tissue was maintained through serial transfers over several months. Heart explants from the cod vigorously pulsated in tissue culture.

INTRODUCTION

It is difficult to imagine a scientific discipline more fascinating than the study of marine life. Through centuries of development and adaptation in accordance with the innumerable changing environments found in the oceans, marine animals present the greatest diversity and numbers of species still to be found (Fox, 1960). The phylogeny of many organs and tissues, simple in structure and in function, precedes the complex highly developed counterparts found in terrestrial animals (Brown, 1957).

Marine and freshwater fish have diseases and ailments which in many cases resemble those commonly associated with higher animals. Platyfish-swordtail hybrids (*Xiphophorus maculatus* × *Xiphophorus helleri*) spontaneously develop melanoma in predetermined areas in the fish (Greenberg, 1956); a neoplasm closely related to melanoma in the human. Certain fish, especially European carp and related cyprinids, may develop an epidermal disease called fish pox, histologically analogous to true neoplasms, which for some yet unknown reason usually regresses and disappears entirely (Nigrelli, 1952). Spectacular and common is a viral disease, lymphocystis, which causes certain cells of both marine and freshwater fish to enlarge from the usual 10 to 50 microns up to 5000 microns or more.

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The husbandry of fresh water fish in hatcheries has included, of necessity, a study of many fish diseases. Many of these diseases are thought to be of virus origin and thus the need arose for virus susceptible cell lines to be used for diagnosis. Normal tissues from trout have been cultivated successfully by Wolf and Dunbar (1957) using the standard tissue culture preparations and sera employed for warm-blooded animals. Among several interesting observations, these authors noted that trout tissues must be cultured at temperatures below 22° C, a temperature considerably colder than that required for mammalian cells. Wolf and Quimby (1962) established a line of trout gonadal cells which are highly susceptible to the virus of infectious fish pancreatic necrosis. The culture of fresh water fish tissue has been extended recently by the report of Clem *et al.* (1962) to include the cells from marine teleosts. The fishes studied by the latter investigators were the yellow-striped grunt (*Haemulon flavolineatum*), the black angelfish (*Pomacanthus* sp.), the porgy (*Calamus* sp.), the pork fish (*Anisotremus virginicus*), the red snapper (*Luljanus* sp.) and the sand perch (*Diplectrum formosum*).

The purpose of this investigation is to attempt to culture marine fish cells from a number of species of fish commonly caught in the cold waters off the Canadian Atlantic coast.

MATERIALS AND METHODS

The fish were caught alive and held in aquaria until used. Tissues were obtained from sexually mature Atlantic cod (*Gadus morhua*), white perch (*Roccus americanus*), winter flounder (*Pseudopleuronectes americanus*), thorny skate (*Raja radiata*), American goosefish (*Lophius americanus*), pollock (*Pollachius virens*) and shorthorn sculpin (*Myoxocephalus scorpius*).

The fish were anaesthetized with M.S. 222 (tricaine methanesulphonate)[4]. The tissues were aseptically removed, placed in 5 ml of Medium 199 containing 50 units/ml penicillin, 50 units/ml streptomycin, and 25 units/ml mycostatin, and cut with scissors into explants roughly 2 mm square. Stationary cultures with fluid media were prepared in plastic tissue culture flasks[5] (30 ml) containing 10 to 30 explants. The freshly transferred tissues were left for periods of up to one-half hour before the addition of the medium[6] to permit the explants to fasten themselves to the plastic surface. All operations and manipulations were carried out in a temperature controlled room at 20° C. Two ml of growth medium was added to each flask. Various growth media, incubation temperatures, and gaseous atmospheres were used in an effort to select a general medium and condition for the survey of tissues from fish. The media were generally renewed every four days. Much of the preliminary investigations were carried out with cod because of its local economic importance and availability.

[4]Sandoz Pharmaceuticals, Dorval, P.Q., Canada.

[5]Falcon tissue culture flask obtained from Becton, Dickinson and Company Canada Limited, Toronto 10, Ontario.

[6]Media were obtained from Becton, Dickinson and Company (B-D) and from Difco Laboratories, Detroit 1, Michigan, U.S.A.

RESULTS AND DISCUSSION

Temperature of Culture Incubation

The temperature of the body of a fish approximates that of its environment which would be for these locally caught fish in the neighbourhood of 3° C to 15° C for winter and summer, respectively. Teleost epidermal tissue very rapidly responds *in situ* to injury caused by a cut or an incision by producing a mixture of mucilaginous material and cells at the edge of the injury. It was noted that fin explants also release or form large quantities of mucilaginous material and cells at the cut edges. Thus the visible production of mucus and the condition of the cells were considered a tentative means for indicating normal tissue response to injury.

Explants of cod dorsal fin were incubated at 5, 20, 25 and 37° C in basal Eagle's medium with double the concentration of the previously mentioned antibiotics in a normal atmosphere. The media containing the explants were stirred slowly with a magnetic stirrer overnight. The condition of the explants and the production of mucus and cells were recorded. When the incubation temperature was 5° C all of the explants were surrounded by a heavy exudant of mucus. All of the cells released from the explant were contained within the mucus and appeared to be healthy. At 20° C a reduced amount of mucus surrounded the explants and both healthy and dead cells were found with the mucus and free in the medium. However, at 25° C there was very little mucus and at 37° C no mucus occurred around the explants. A great number of cells and debris were present in the medium at both incubation temperatures. The cells released at 25 and 37° C did not appear healthy and many were breaking down. The bacterial population was controlled with the previously mentioned antibiotics. (The bacterial flora of fin tissue from fish obtained commercially could not be controlled with the above antibiotics.)

It is likely that a number of interpretations can be given to these data such as the solubility of mucus at the various temperatures. However the production of mucous substance by cells and its presence as a matrix for cells has been suggested as being necessary to provide cells with a controllable microenvironment (Moscona, 1959). In addition, if cod dorsal fin explants are incubated at 5 and 20° C, respectively, in the same medium without stirring, the explants at 5° C generally show good cell attachment and proliferation within 24 hours, whereas the explants incubated at 20° C generally show only limited cell attachment and proliferation. There was no growth at 37° C. A statement of caution has to be noted here: growth response varies greatly from explant to explant from the same tissue and from explants from the same tissue from different fish. A more accurate evaluation of temperature response may possibly be obtained by using an established line of cells. However, even here there may be the danger of cell selection. Thus the incubation temperature of 5° C was adopted, with reservation, as the most desirable temperature to assess the culture of tissues and organs of these fish.

Growth Medium

Because of the variable proliferation response of cod fin tissue, it was impossible to state with confidence which medium was most suitable for growth. Instead, it was only possible to choose the medium which appeared to support the greatest, most rapid and sustained cell proliferation. For example, limited attachment and growth also occurred in synthetic medium, such as basal Eagle's medium, Eagle's Hela medium, Medium 199, and Medium 1066. However, by augmenting these latter synthetic media with various animal sera and extracts it was noted that in general Medium 199 containing one of several sera supported the best growth. It was also noted that equivalent or possibly better growth was obtained under an atmosphere of air than under atmospheres of 5% CO_2:air; 5% CO_2:28% O_2:air; 5% CO_2:36% O_2:air; or 5% CO_2:60% O_2:air. The incubation of cultures in an atmosphere containing 5% CO_2:air is recommended to buffer culture medium in the range of pH 7.2 to 7.4. The final pH of the nutrient solution containing Medium 199 and the animal sera was in the range of 7.2–7.6, depending on the serum. Variation of pH within this latter range did not noticeably alter growth response. An example of typical cell proliferation from cod dorsal fin explants in various animal sera and extracts in Medium 199 under normal room atmosphere at 5° C is shown in Table I. Bovine serum, beef

Table I. Comparison of the proliferation of cells from cod fin explants cultured in various fluids[1].

Supplement	Response[2]
Chicken plasma (B-D)	++
Bovine serum (B-D)[3]	+++
Human ascitic fluid (Difco)	+++++
Human serum (Difco)	+++++
Chicken embryo extract (B-D)	+++
Calf serum (B-D)	+
Sheep serum (B-D)[3]	++
Beef embryo extract (B-D)	++++
Horse serum (B-D)[3]	+
Beef amniotic fluid (B-D)[3]	+

[1]The medium was composed of Medium 199 containing 10% of the animal fluids listed and antibiotics. The cultures were incubated at 5° C.

[2]Growth = +; luxurious growth = +++++

[3]Only one sample of supplement was tested.

embryo extract, human serum and ascitic fluid consistently supported better cell proliferation than did the other sera. The human and ascitic fluid sera were considered about equal and generally better than either beef embryo or bovine serum. Human serum was chosen as the medium with which to determine growth response in other tissues. It is realized of course that the latter medium may

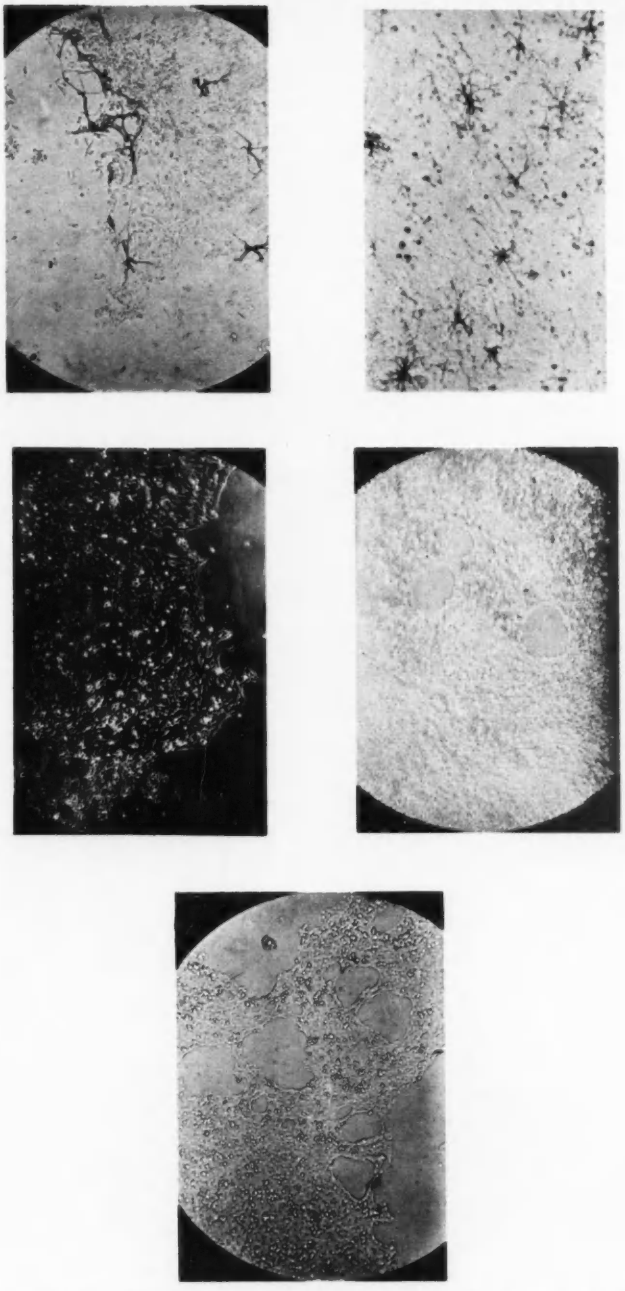

FIG. 1. Photographs of cell proliferation from teleost fin tissue: *top left* — Cod fin (× 35); *top right* — Pollock fin (× 56); *centre left* — Flounder fin (× 35) phase contrast; *centre right* — Goosefish fin (× 35) phase contrast; and *bottom* — Perch fin (× 35).

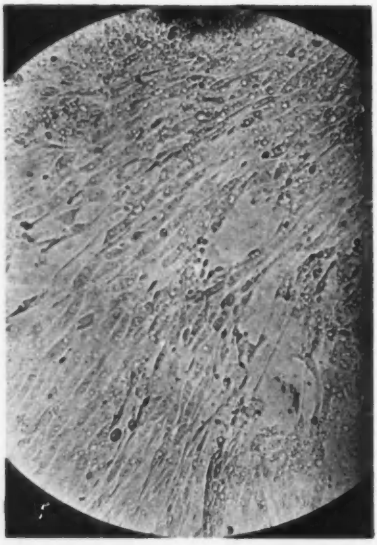

FIG. 2. Photograph of cell proliferation from skate heart tissue (× 140).

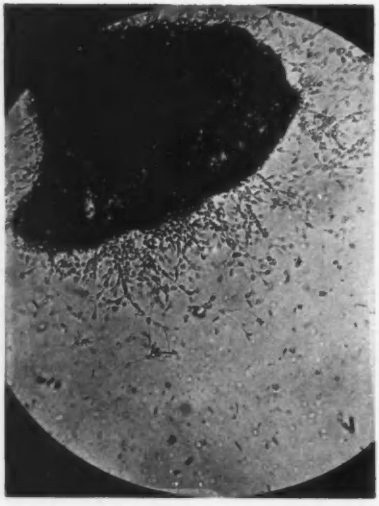

FIG. 3. Photograph of cell proliferation from sculpin spleen (× 45).

FIG. 4. Photograph of cell proliferation from pollock kidney (× 64) phase contrast.

not be the most desirable medium for other tissues, and that individual specimens of mammalian sera may show toxicity to cell cultures (Parker, 1961).

Attachment and Growth of Fish Tissues

During preliminary investigations chicken plasma coagulum was used as a matrix for the support and attachment of cod cell outgrowth from explants. This culture method was soon abandoned in favour of the stationary fluid culture technique because of the tedious nature of preparation and the ability of the fish explants to securely fasten themselves to the culture dish surface in the absence of a plasma clot. There did not appear to be any significant difference in growth response between the two culture methods.

Table II. Cell outgrowth from marine fish tissue explants[1].

Fish	Fin	Spleen	Heart	Kidney	Liver	Gonad	Other Tissues
Cod	+	+	-	+	+	+	Thymus, brain
Flounder	+	+	+	+	+		
Pollock	+	+	+	+	-	+	
Goosefish	+	+	+	-	+		Bait, brain
Sculpin	+	+	+	+	-	+	
Perch	+	-	-	-	-	-	
Skate	-	+	+	+	-	-	Uterus

[1]The culture medium contained Medium 199 + 10% human serum and was incubated at 5° C (growth = +; no growth = -).

Luxurious outgrowths were observed from all fin tissues except from the fin of the skate (Fig. 1). The primary culture of the cod fin may be kept viable and proliferating for at least six months. No attempt was made at subculturing beyond a single transfer. The reason for the growth difference between the fin of the skate and the other fish fins is unknown except that the skate is of course separated taxonomically from the true fish (Table II). On the other hand the heart tissue of the skate provided abundant outgrowth as did the heart tissue from the flatfish and the sculpin (Fig. 2). Both the spleen and the kidney provided good explant outgrowth with the exception of perch spleen and kidney and of goosefish kidney (Fig. 3 and 4). Flounder kidney cells freed from explants by mechanical disruption have been successfully transferred several times over a period of many months. Cell preparations obtained by the application of trypsin or collagenase enzymes on kidney explants did not proliferate.

Explants of brain did not show growth within two weeks with the exception of several explants from the goosefish. However, after several months incubation during which time the medium was not renewed abundant cell proliferation was noted for the brain explants of the goosefish and the cod. Similarly, liver explants of the cod, flounder and goosefish, particularly the latter provided good cell outgrowth after a similar long period of incubation without renewal of the medium. These liver cells contained a large number of oil-like globules.

Another rather interesting observation was noted with the heart explants of the cod which after approximately one month of incubation without medium renewal were observed at 20° C to violently pulsate in a regular fashion, one beat every two to three seconds. Several areas of an explant were observed to pulsate independently at different rates for several hours then the beat would weaken or tire. Regeneration of the strong pulsation could be obtained by re-incubation of the tissue at 5° C overnight. This temperature-dependent re-energizing of tissues capable of contraction has also been noted as the reason for systaltic action in kidney tubules, possibly an important event in kidney function (Townsley and Scott, 1962).

REFERENCES

BROWN, M. E. [Editor] 1957. The physiology of fishes. Academic Press, Inc., New York, Vols. 1 and 2.

CLEM, W., L. MOEWUS AND M. M. SIGEL. 1962. Studies with cells from marine fish in tissue culture. *Proc. Soc. Exp. Biol. Med.*, **108**: 762–766.

FOX, D. L. 1960. Perspectives in marine bicchemistry. *Ann. New York Acad. Sci.*, **90**: 617–621.

GREENBERG, S. S., M. J. KOPAC AND M. GORDON. 1956. Cytology and cytochemistry of melanoma cells. *Ann. New York Acad. Sci.*, **67**: 55–122.

MOSCONA, A. A. 1959. Patterns and mechanisms of tissue reconstruction from dissociated cells. Cited in "Developing cell systems and their control". Edited by D. Rudnick, The Ronald Press Company, New York, p. 52.

NIGRELLI, R. F. 1952. Virus and tumors in fishes. *Ann. New York Acad. Sci.*, **54**: 1076–1092.

PARKER, R. C. 1961. Methods of tissue culture. Paul B. Hoeber, Inc., 49 East 33rd Street, New York 16, N.Y. 3rd ed.

TOWNSLEY, P. M., AND M. A. SCOTT. 1962. Systaltic muscular action of the kidney tubules of flounder (*Pseudopleuronectes americanus*). *J. Fish. Res. Bd. Canada*, **20**: 243–244.

WOLF, K., AND C. E. DUNBAR. 1957. Cultivation of adult teleost tissues *in-vitro*. *Proc. Soc. Exp. Biol. Med.*, **95**: 455–458.

WOLF, K., AND M. C. QUIMBY. 1962. Established eurythermic line of fish cells in vitro. *Science*, **135**: 1065–1066.

Effects of Temperature on Growth of Zooplankton, and the Adaptive Value of Vertical Migration[1]

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ABSTRACT

Existing theories of the adaptive value of vertical migration are examined and found wanting. Adult size and generation length are negative functions of temperature. It is shown that Bělehrádek's temperature function gives a close fit to size and development rate of several species of zooplankters growing in adequate food supply, although conclusions do not depend on the theoretical content of this equation. Fecundity is an exponential function of adult size, and enough data are available for two quite different zooplankters — the copepod *Pseudocalanus minutus* and the chaetognath *Sagitta elegans* — to depict relative rates of increase as generally positive functions of temperature. Diurnal migrants are known to feed nearer the surface, which is almost universally warmer. Increased fecundity gained by spending part time in deeper, cooler waters, might be offset by slower development, although interrupted or seasonal breeders could sacrifice development rate for greater ultimate fecundity. However, an animal which does all necessary feeding in warm surface waters and "rests" in cooler waters gains an energy bonus which may be put into fecundity. A model of the effect on fecundity is derived from a much-generalized version of von Bertalanffy's growth equation. From the most probable range of solutions it is deduced that migration in thermally stratified waters would be disadvantageous when surface waters were cool, but increasingly advantageous as surface waters warmed up, and this is supported by empirical evidence. The theory accounts for many geographical, seasonal, systematic and ontogenetic regularities in the large and confusing literature on vertical migration.

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EXISTING THEORIES ON THE ADAPTIVE VALUE OF VERTICAL MIGRATION

THE LITERATURE on the vertical migration of zooplankton is enormous, complex, and full of conflicting observations and generalizations. A considerable amount of observation and experiment suggests that light is generally the initiating, controlling and orienting factor in migrations, although anomalies are known, with the effect of light being modified by other physical and biological factors. On the other hand, there are several theories, some very ill-formed, on the adaptive value of vertical migration. Some of these theories are outlined briefly here, for they are given in several recent reviews (Cushing, 1951; Hardy, 1956; Bainbridge, 1961). Most of the discussion in the literature concerns diurnal vertical migration, although seasonal and other migrations have been considered, and even incorporated into more general theories of the adaptive value of such activities.

It has been common in the literature to refer to animals as seeking "optimum" light intensities. Although some authors seem to imply that this is an adaptive end in itself, the word can generally be taken as meaning "the same" light intensities. Even then, movements often seem poorly correlated with absolute light levels (Clarke and Backus, 1956). Although light as such might be deleterious to organisms at the immediate surface, the only general value in leaving the upper waters during daylight hours seems to be the obvious one—escape from potential predators. The upper waters are food-rich, but dangerous by day; herbivores are forced to secure their food there by night, and carnivores, if they themselves are not likewise prey, follow the behaviour of their food species. Although this idea has had a long history and is still current (e.g. Manteufel, 1959), it has received remarkably little attention or support from most of those who have reviewed the subject at large. This appears to be because this simple theory becomes less attractive as more is known of vertical migration. Granted that potential predators might see their prey in light down as low as 10^{-10} times the daylight surface values (Clarke, 1936), most migrants do not seem to go sufficiently deep. Granted further that any amount of light reduction would offer some protection, certain migrants seem to go far beyond what must be effective total darkness for seeing prey (see examples in Moore, 1958). Indeed, Waterman (1960) has recently pointed out that vertical migration may occur at depths where no light could be detected, let alone used in seeing prey. And why should many migrants be luminous? Further, the phenomenon is by no means as universal as predation itself must be. Why should animals live continuously near the surface during 24-hour daylight in the arctic? There is enough diurnal light variation to provoke a response, but it could be argued that half the usual time spent in darkness (and about half the selective value?) might not be enough. However, recent work has shown copepods in the upper waters of the tropical Pacific also to be mostly non-migratory (see p. 712). Why should normally migratory species be found at the surface in full sunlight at some seasons? Why should the young of most migrant species be themselves non-migratory, even although, if anything, young animals would be subject to greater predation by

the numerous young of predators? Why, for example, should *Calanus* copepodite III, which is much larger and faster than many migrant species, live continuously near the surface, while the next stage, copepodite IV, only some 25% longer, undertake diurnal migrations of over 100 metres?

Doubtless escape from predators could be an element in the adaptive value of migration. It is probably the essential reason for descent by day rather than by night, although an interesting exception will be noted later (p. 713). But the fact that behaviour may be greatly modified and the habit even dispensed with in a variety of circumstances has led authors to seek more compelling and general reasons for vertical migration. If anything, there has been an acceleration of theorizing in recent years.

A group of theories has been built around the value of vertical migration in mediating the horizontal distribution of animals. The animals are thought to take advantage of vertical differences in direction and velocity of water movements.

It has been suggested by some authors that vertical migration may permit navigation, in the strict sense of that word. It is hard to believe that the current structure of waters would offer such a navigational advantage very often, but several authors (e.g. Mackintosh, 1937) have described settings where seasonal migrations between countercurrents might fulfill this function. It might also be effective in maintaining populations in estuaries.

As originally proposed (Hardy and Gunther, 1935) horizontal displacement resulting from vertical migration was supposed to enable animals to avoid hypothetical toxic effects of dense patches of phytoplankton. Although such toxicity is no longer hypothetical, it has become increasingly evident that herbivorous zooplankton in nature by no means tends to avoid dense phytoplankton. Much of the patchiness and local differences in zooplankton–phytoplankton balance which exist in nature are the product of well-ordered relationships between the growth of plants and grazing by zooplankton (see Beklemishev, 1957, for a wealth of examples; and Steele, 1961, for a far-seeing theoretical treatment). Most recent authors, therefore, including Hardy (1956), seem to prefer the view that vertical migration aids herbivores in exploiting denser patches of phytoplankton in surface waters. Predacious zooplankton is supposed to follow the behaviour of its herbivorous prey. A qualitative model of the means by which vertical migrants may congregate in dense patches of food was developed by Bainbridge (1953). In order to congregate in dense patches of phytoplankton, the animals have to respond to the amount of food by modifying the extent of vertical migration, even by giving it up. There is no unequivocal evidence that vertical migration is most pronounced when food is locally scarce or that it ceases when food is most abundant. The general objection to these ideas is that vertical migration seems a remarkably regular and widespread phenomenon to have arisen under what must be spatially and temporally a most irregular and elusive selective demand. In regions where phytoplankton flowerings are markedly seasonal and where patchiness results because local areas are

out of phase (the "seasonal" effects discussed at length by Beklemishev, 1957), it can be seen that any animal which maintained its position would sooner or later benefit from the local cycle, while the success of one which abandoned its position would be a function of its horizontal velocity and the distance between patches. The quantitative aspects of this problem have not been considered, but there are other difficulties. The grazing down of a geographically localized patch of phytoplankton is accompanied by a sequence of maturation, reproduction and brood growth in response to food supply, at least in short-lived forms such as copepods. The advantage would appear to lie with those animals which were present from the beginning of the flowering. This argument is further reinforced by the fact that in animals in which ontogenetic studies have been made, the youngest stages are non-migratory. This could be taken to mean that, not only would later arrivals at a phytoplankton patch be less likely to find adequate food, but their young would be less likely to have the putative means of escaping the deteriorating conditions. The theory that migration aids access to food, which has been developed by students of marine zooplankton, also seems much less plausible when applied to small lakes, whose vertical migrants may arise from the depths to feed in a thoroughly mixed euphotic zone, where phytoplankton patchiness may be absent. Altogether, these seem to be internal inconsistencies in the theory which have not been properly dealt with.

Recently David (1961) has made new use of the general idea that vertical migration may affect horizontal position. It is clear that species must strike an adaptive balance between too much and too little genetic recombination (see Carson, 1957, for a recent discussion), and David supposes that the forces of diffusion in the aquatic habitat provide insufficient opportunities for exchange. His hypothesis is that "mixing by vertical migration inhibits the formation of too many species with too little capacity to survive changes in the environment". He points out that if all animals migrate synchronously, or even spend equal amounts of time in the same layers, then there is no mixing value. Indeed, as Hardy (1956) has shown, synchronous migrations of a horizontally uniform population may result in its breaking up into patches, which would decrease the gene flow between groups. David therefore seems to suggest that it is the *lack of synchrony* found in migrating populations which is the adaptive character of vertical migration. Presumably in its turn this polymorphism of behaviour can be considered to be maintained by variable adaptive values. Unfortunately, David does not appear to have considered the rigorous limitations on any system involving selection of traits. If it is his contention that vertical migration serves *only* the longer term advantage of facilitating gene flow, then, since movements through suboptimal strata must occur, the immediate advantage would go to any non-migrants or limited migrants living in the strata with optimal conditions. This population would probably not be small enough to suffer from "genetic drift", and would be subjected at least to seasonal changes to preserve a certain adaptability, whether at the individual or population level. But, even if it were forced to become dangerously specialized, as David supposes, such a population could continue to make full use of the gene pool of migrant members of the

species *without incorporating the immediately non-adaptive migratory traits.* Either wholly *ad hoc* reproductive barriers must be raised, or such an adaptive system is clearly unstable and internally inconsistent. David's theory also seems inadequate to explain certain facts; for example, it seems quite out of the question that vertical migration could serve to enhance recombination in planktonic Cladocera, which exhibit such marked suppression of sexuality. It is also instructive to consider the three pelagic copepods which are probably the most abundant in northern seas—the *Calanus finmarchicus* group, the *Pseudocalanus minutus* group, and the *Oithona similis* group. They are called "groups" advisedly for, although even in quite recent works each is usually considered to be cosmopolitan in colder waters, it is probable that more than one species is included under each name. *Oithona similis* is a surface dwelling form, and the only one of the three which performs little or no vertical movement (see p. 713). Although doubtless due partly to the relative attention which these groups have received (especially by Russian workers), the *C. finmarchicus* group is listed in recent years as the most polytypic, and *O. similis* the least. It can only be said that there is no evidence that the least migratory form is more prone to speciation or less successful than the two migratory ones. One may therefore agree with David's own modest appraisal of his hypothesis that it is "regretably speculative and what evidence there is which might support it is both slight and circumstantial", and seek a more immediate adaptive value for vertical migration.

The most recent theory we have to consider is that presented in a chapter on vertical migration in the controversial book by Wynne-Edwards (1962). I do not think it is a parody of his views to summarize his theory as follows: animals by periodically moving vertically concentrate themselves near the surface by night, although sometimes by day and sometimes at other levels in the water column (e.g. thermoclines), in order to carry out social ("epideictic") displays which serve to plot the reproductive strategy of the population. By sensing their population density, animals limit the rate of increase to prevent the catastrophic reduction of available resources. It is not possible to consider Wynne-Edwards' general theory of animal control here, but it is sufficient to say that there is simply no evidence for the social control of the intrinsic rate of increase of zooplankters. Key statements such as that *Calanus* "is fecundated early in the season and can control the emission of eggs over the next few months" are gross distortions of the facts. Evidence from crowded laboratory populations of *Daphnia* quoted elsewhere in his book can be dealt with in terms of energy shared from a limited resource (the same data being thus analyzed by Slobodkin, 1961a). Indeed it will be clear that examples of rate of increase given in this paper are explicable in terms of food and temperature, and sometimes temperature alone.

A unique but rather unhappy solution to the problem is offered by Harris (1953). He believes that the habit is devoid of adaptive meaning as such, but simply a side-effect of a light-controlled means of maintaining optimum depth (however defined) within the euphotic zone. This is a regression to ideas held by some of the earlier experimentalists on the subject, and is especially unlikely,

as Hardy (1956) and others point out, because optimum depth could be maintained with less effort by pressure sensitivity, known in some forms.

Finally, among students of vertical migration, Moore and his co-workers in a series of papers have emphasized the complex interaction of several factors in vertical migration. Temperature has seemed to them to be of great importance in modifying such movements and establishing boundary conditions. After citing evidence that organisms exposed to fluctuating temperatures may show improved development and survival, and suggesting that different physiological processes may benefit most from different temperatures, Moore and Corwin (1956) are tempted to speculate that "the importance of vertical migration lies in the attainment of such alternation of temperature". It will be obvious to the reader that Moore and his co-workers have been on the verge of stating some of the ideas in this paper.

TEMPERATURE AND GROWTH

Introduction

The influence of temperature on metabolism and growth of poikilotherms has received much attention in the laboratory and in the field. Many field observations support the generalization that animals of high latitudes develop more slowly and reach a larger size than their counterparts in warmer climes. Such studies are complicated by geographical adaptation, which may be responsible for such notions as the existence of optimal temperatures for largest size in some species. For this reason I will not consider the large literature on latitudinal differences in growth and metabolism (but see the review by Dunbar, 1957).

We are interested in two aspects of growth for the present purposes: adult size and development rate through life. In the following sections use will be made of an analytical expression relating these aspects of growth to temperature. This expression, developed by Bělehrádek (1935), has been largely ignored or misused in subsequent studies of the effects of temperature. The justification for its use here is empirical: that is, the calculated curves fit the data I use better than other possible analytical curves, and virtually as well as "eye-fitted" ones, but are much easier to use than the latter in further equations. The reader may judge for himself its empirical utility from examples illustrated in this paper, but the conclusions reached do not depend on any theoretical content of this function. While I use this function as though it had a certain universality, the same conclusions could be reached by using eye-fitted curves, with much more calculation, and with perhaps one or two further assumptions. However, in view of the many formulas which have been used in the large literature on temperature effects, it seems necessary to review them and give some mathematical and biological reasons for choosing one expression above the others. As this is not necessary to the substance of the paper, it is done in the Appendix.

The form of Bělehrádek's function is:

$$V = a\,(T + \alpha)^b \qquad \ldots\ldots(1)$$

where V is the velocity of the process, T the temperature in degrees Celsius, and a, b and α are constants. The value of a depends on the units of V, b reflects the degree of curvature and α is a scale correction, referred to by Bělehrádek as the "biological zero", which bears no relation to zero Celsius, but gives the temperature at which V = 0. The function has been fitted in all examples given here to the value of α giving the least mean squares deviation.

The Effect of Temperature on Generation Length

Although the effect of temperature on development rate of such animals as insects has been dealt with quite commonly, suitable data on zooplankters are much scarcer. There are many qualitative estimates from nature, but the only example known to me in which food might not have been an important influence is that given by Woodmansee (1958). Woodmansee graphed the relationship between generation length of the copepod *Acartia tonsa* and temperature in southern Florida, where food *might* be seasonally more uniform than in boreal waters. The points are few and scattered, and the inverse linear relationship fitted by Woodmansee over a range of about 10°C is open to doubt.

There is little more information available from the laboratory, and most of it, as might be expected, deals with early development. The effect of temperature on the time taken to hatching of eggs of the rotifer, *Ploesma truncatum*, from Lago Maggiore in Italy (Edmondson, 1960) is well expressed by Bělehrádek's function (Fig. 1a). The only such information apparently available from a copepod, *Calanus finmarchicus* (Marshall and Orr, 1953), is also well-served by Bělehrádek's function (Fig. 1b), although it is probable that 20°C is outside the normal range of temperature for this species in northern Norway.

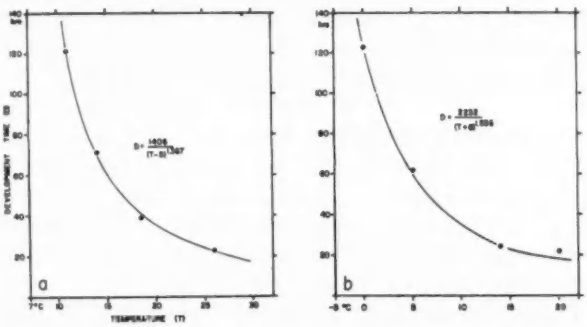

FIG. 1. Effect of temperature on time taken for development to hatching of two zooplankters: (a) the rotifer *Ploesma truncatum* from Lago Maggiore, Italy (unweighted means from Edmundson, 1960) and (b) the copepod *Calanus finmarchicus* from Tromsø, Norway (weighted means from Marshall and Orr, 1953).

Granted that Bělehrádek's function is useful in describing development rate of a single stage, such as the egg, is it likely to be adequate for length of a generation made up of a succession of stages, each of which might have different temperature characteristics? Only two examples seem to be available, both

from the Cladocera, in which length of life was studied as a function of temperature in the presence of adequate food. It is gratifying to see that both *Daphnia* (MacArthur and Baillie, 1929) and *Moina* (Terao and Tanaka, 1930) can be handled by this equation (Fig. 2 a and b). *Moina* offers one of the very few examples of shortening of length of life at low temperatures. Earlier work by the authors showed that parthenogenetic reproduction ceased at about 8–10°C, and probably the animal normally exists as resting eggs. At any rate, we may agree with Shaw and Beauregard (1962), who have recently argued from empirically questionable Arrhenius functions fitted to the data in Fig. 2a, b, that the shortening of life at low experimental temperatures is "unphysiological".

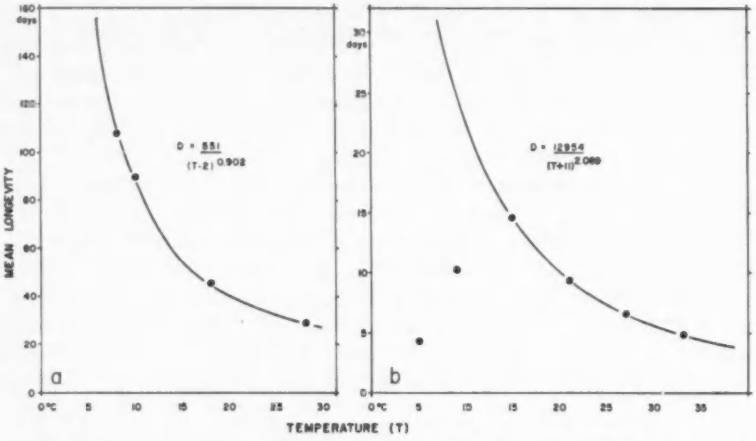

FIG. 2. Effect of temperature on mean length of life of two Cladocera: (a) *Daphnia magna* (unweighted means from MacArthur and Baillie, 1929) and (b) *Moina macrocarpa* (unweighted means from Terao and Tanaka, 1930).

THE EFFECT OF TEMPERATURE ON ADULT SIZE

There is much less suitable information concerning the effect of temperature on size than on developmental or physiological rates. Before the effect of temperature can be dealt with, the role of food supply must be considered.

It is known that food supply can account for differences in final length of some 20–25% in *Daphnia* (e.g. Ingle *et al.*, 1937; Richman, 1958). However, this does not appear to be true of all planktonic animals. Coker (1933) set out to test a prevailing notion that a reduction of food supply for copepods would produce dwarfed adults. It is difficult to extract quantitative conclusions from his work on several species of *Cyclops*, but it can fairly be said that large reductions (by 10-fold or more) of food supply could slow down development or thwart it altogether—animals not developing beyond copepodite IV or V during an experimental period 6 times as long as normal development at that temperature. On the other hand, food shortage did not effect a reduction of length of the adult stage, when this was reached, of more than about 10%, whereas raising the growing temperature from 8 to 28°C decreased adult length by 35–45%. Unfortunately,

in experiments on *Daphnia* and *Cyclops*, only a few temperatures have been used and only a few animals grown at each temperature. Although sufficient to demonstrate a marked negative correlation of size with temperature, the relationships show a great deal of scatter.

Deevey's (1960) important statistical study concluded that temperature alone could account for size of copepods in marine waters with a wide seasonal temperature range, but that amount of food was also important in waters with a narrower temperature range. This does not at first sight conform to Coker's (1933) laboratory findings that excessive reduction of food stopped development rather than "permit" maturation at a significantly smaller size in freshwater copepods. I believe that the effect of food on adult size demonstrated by Deevey is an indirect result of temperatures acting during retarded development. In almost all regions studied by Deevey, adult copepod size was less strongly correlated with temperature and food at the time of sampling than with average temperature and food quantity during the month preceding the sampling date. She concluded that final size is determined by conditions prevailing during at least part of the development period, and not merely by conditions at the time of the last moult. In all localities from which measurements were available, food supply was negatively correlated with temperature. This means that size might be more closely correlated with immediate temperatures when these are low due to food-accelerated growth, and this form of dependence cannot be eliminated by the partial correlations used by Deevey. It seems clear that a complete study should consider conditions during the whole period of development, and fortunately sufficient information is available from one locality.

An example of the effect of food on size was derived by Deevey from data on temperature, phytoplankton and size of copepods in Loch Striven, as published by Marshall (1949) and Marshall *et al.* (1934). The same works contain information on the duration of generations through the season, and data for the copepod *Pseudocalanus minutus* are given in Fig. 3. It can be seen that the correlation of adult size with average temperature during the preceding month is greater than with temperature at the time of sampling ($r = -0.689$ and -0.507 respectively, per Deevey). It may be assumed, with Deevey, that development is completed in roughly a month in spring and early summer, but this is not true for the whole year. For example, Marshall (1949) gives evidence that small adults found at the end of winter had been developing, however unevenly, from about mid July of the previous year, and that large adults appearing in early April were born beginning in mid February. Using such information we may plot mean size of female *P. minutus* on each collection date against mean temperature during development. Even although temperatures have been grossly interpolated between early September and late January, and even although mean temperature may be quite inadequate to express the effect of temperature during interrupted or irregular development, the relationship in Fig. 3d is remarkably regular. This example is strong support for the contention that food affects primarily development rate, but has little direct effect on final size, at least in copepods.

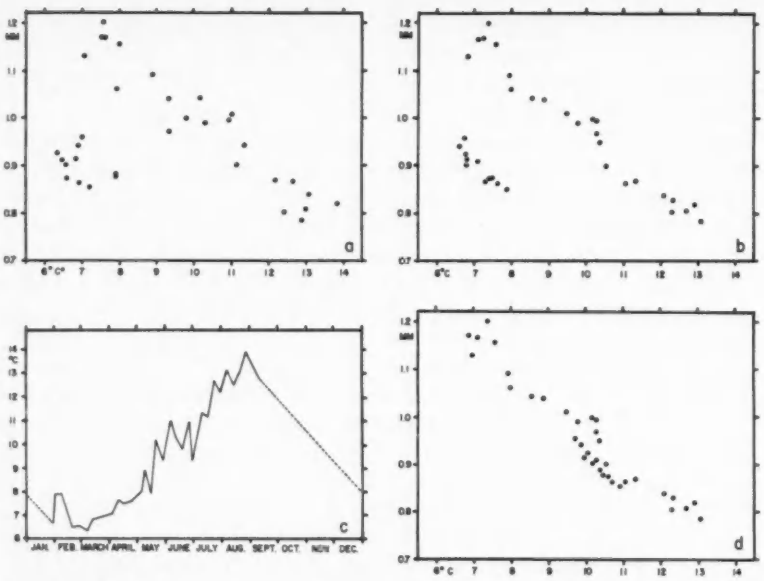

FIG. 3. Mean cephalothorax length of female *Pseudocalanus minutus* in Loch Striven plotted against temperature at time of sampling (a), mean temperature of the previous month (b), and mean temperature during the lifetime of each generation (d), determined from data in (c), which shows mean of temperatures at the surface and 30 m. Data from Marshall (1949), and Marshall *et al.* (1934).

Thus in choosing examples to demonstrate possible analytical relationships between size and temperature, we must have information on temperatures during the development period. Since mean temperature may be inadequate, the best examples would be ones in which food was always plentiful, and animals therefore developing rapidly at temperatures differing little from those at the time of sampling. For reasons which will be clear later (p. 711), the water in which the animals are living should not be thermally stratified; even the average temperature at which the animal lives in the water column cannot be used directly. Of all the copepod material analyzed by Deevey (1960), the only suitable data come from Long Island Sound. Here growth was rapid, and a 10-fold variation in food supply had no statistical effect on final size of the four species of copepods which were studied. There is also very little thermal stratification in Long Island Sound during the growing season (Riley, 1956), which is not true of other localities studied by Deevey. Two of the four species from the Sound showed better correlation of size with temperature at the time of sampling than with mean temperature of the previous month, and in fact gave larger negative correlation coefficients than any other populations analyzed by Deevey. These are *Acartia clausi* (Fig. 4) and *Pseudocalanus minutus* (Fig. 5). Even although no rationale for fitting the same function to size as to rates is given here (one will be given later, p. 708), the relation between size and

temperature in these species is obviously non-linear, and seems well described by Bělehrádek's function ($r = -0.965$ and -0.977 compared with linear coefficients of -0.950 and -0.957 for *A. clausi* and *P. minutus* respectively). Note that the biological zeros are comparable to that calculated for development of *Calanus finmarchicus* (Fig. 1b) which is exposed to about the same minimum temperatures in nature. Figure 6 clearly supports Deevey's contention that the residual scatter in these size–temperature relations is not due to food supply.

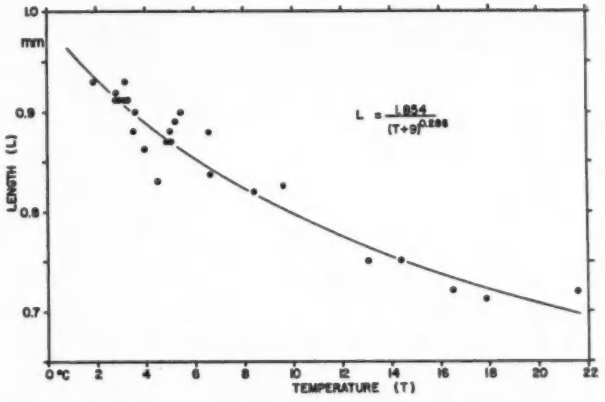

FIG. 4. Relationship between mean cephalothorax length of female *Acartia clausi* and temperature at the time of sampling in Long Island Sound (after Deevey, 1960).

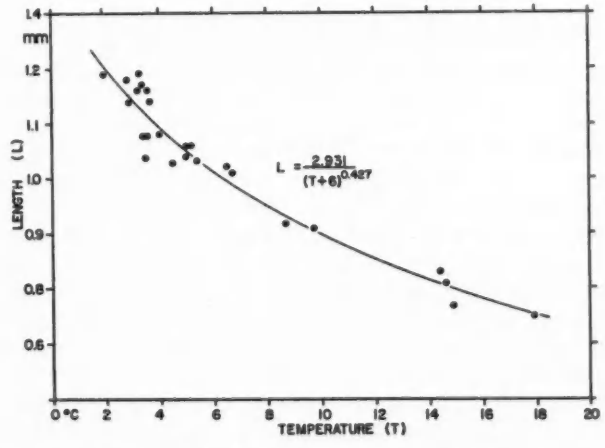

FIG. 5. Relationship between mean cephalothorax length of female *Pseudocalanus minutus* and temperature at the time of sampling in Long Island Sound (after Deevey, 1960).

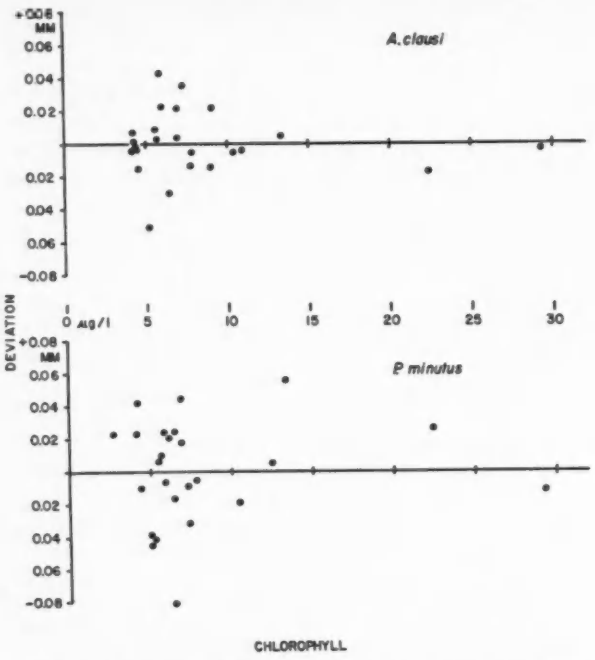

FIG. 6. Relationship between amount of chlorophyll at time of sampling and deviations from the size–temperature curves shown in Fig. 4 and 5 (data from Deevey, 1960).

The study of copepod size by Deevey is simply not matched in any other zooplanktonic group. However, valuable data are given by Russell (1932a, b) on the biology of the chaetognath *Sagitta elegans* in the waters off Plymouth. Russell graphs (1932b, his text-fig. 2) periods of reproduction, average lengths of adults during these periods, and temperature at the surface and 25 m between May 1930 and September 1931. These waters are almost unstratified below the top few metres most of the year, and since *S. elegans* does not as a rule occur at the immediate surface even at night, the temperatures at 25 m may be taken as approximating those to which developing animals were exposed. Thus for several generations of adults there are data on average size (estimated by inspection by Russell), duration of their generations (taken between mid points of successive breeding periods in Russell's figure), and mean temperature during their development. The adult generation in May 1930 may be assumed to have been born in February, as in 1931. Understandably there is a good deal of scatter in the size–temperature relationship, but again it appears to be non-linear, and well fitted by Bělehrádek's function in Fig. 7. The effect of food on growth can be roughly determined. Seasonal values of zooplankton biomass during another year in the same region are given by Harvey *et al.* (1935).

Although there is no way of determining what part of this biomass might serve as food for the predacious *S. elegans*, the relationship between generation length and mean crop of zooplankton is consistent with the suggestion that the effect of temperature on development rate is masked by the effect of food (Fig. 8). On the other hand, food fails to account for the residual scatter in the length–temperature relation (Fig. 9).

These three animals seem to be the only members of the zooplankton for which sufficient suitable information is available, and it must not be imagined that they have been "picked" for any reasons other than those stated. Fortunately, they are representative of two extremely different phyla, and might be taken as models for the zooplankton as a whole.

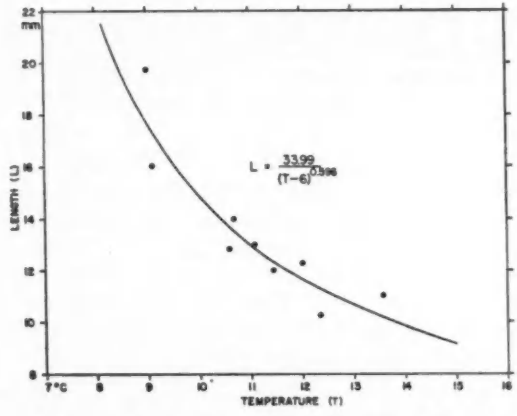

FIG. 7. Relationship between mean length of adult ("stage III") *Sagitta elegans* and mean temperature at 25 m during their developmental periods off Plymouth (data from Russell, 1932a, 1932b).

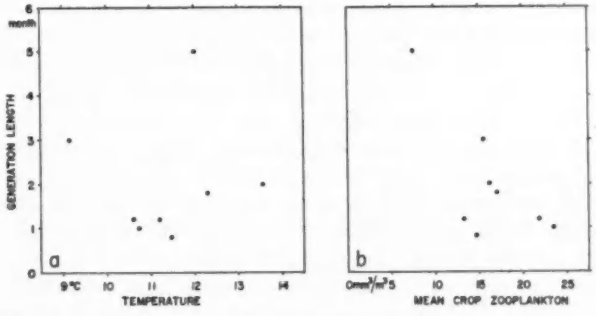

FIG. 8. Generation lengths of *Sagitta elegans* related to temperature (a) and food (b) during their developmental periods off Plymouth (data from Russell, 1932a, 1932b, and Harvey *et al.*, 1934.

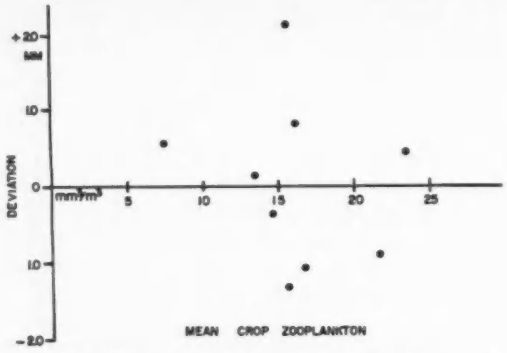

FIG. 9. Relationship between mean standing crop of zooplankton during the developmental periods of *Sagitta elegans* and deviations from the size–temperature curve of Fig. 7 (data from Russell, 1932a, 1932b, and Harvey *et al.*, 1934).

FECUNDITY AND RATE OF INCREASE

Large differences have been noted by many authors in the numbers of eggs carried by zooplankters such as Copepoda (see Hutchinson, 1951) and Cladocera (see Green, 1958), both through the season and within different populations of the same species. Environmental circumstances have not always been clearly indicated, but low clutch size seems often associated with low food supply and high temperatures (which are themselves usually found together seasonally in lakes and in the sea). Some animals are known to produce a single clutch (e.g. Chaetognatha), and others one clutch in each of a fixed number of instars (e.g. Cladocera), so that clutch size is a good measure of fecundity. Most authors seem content to assume that clutch differences reflect fecundity in copepods, but Elgmork (1959) suggests that smaller egg sacs of *Cyclops strenuus* may be produced more rapidly than large ones, to achieve the same total production. Food certainly acts as a stimulus to egg production in many species of copepods, but in *Calanus finmarchicus*, in which it has been experimentally studied (Marshall and Orr, 1955a), there are asymptotes in total production of eggs as well as in rate of laying. This suggests that, given an adequate food supply, the fecundity of a female is in some way fixed.

In a wide variety of poikilotherms, from fish to lobsters, large females are known to be more fecund than small ones. It is not surprising, then, that similar relationships have been found in planktonic organisms. Among copepods, statistically significant positive correlations between female size and egg number have been shown for 2 marine species (Marshall, 1949), 2 freshwater diaptomids in Italy (Ravera and Tonolli, 1956), 4 of 5 diaptomids from Lake Erie (Davis, 1959), and for several species of cyclopoids (Margalef, 1955). Treated as an example of relative growth, it can be expected that the relationship between length and egg number would be:

$$E = mL^n \qquad \ldots\ldots(2)$$

where E is egg number, L length and m and n constants, and this has been indicated for Cladocera by Green (1958). Jensen (1958) has shown for a wide variety of malacostracan Crustacea that egg number is more precisely a linear function of the volume of the female, but this is not true of all groups. Margalef (1955) has derived an interesting empirical formula applying to several species of *Cyplops* which he studied. Where L is the length of the female in millimetres, h the haploid number of chromosomes, and E the number of eggs per ovisac, then:

$$E = \left(15 \frac{L}{h}\right)^3$$

In the chydorid Cladocera, whose clutch size is invariable, a correlation between length and egg size has been shown (Green, 1958).

Since size may be affected by temperature during development, we may confidently expect fecundity to be negatively correlated with temperature during development. The "growth factor" (proportionate increase of length between moults) in copepods under uniform conditions approximates 25% ("Brook's Law"), which suggests a doubling of cell mass. Margalef (1955) makes the further provocative suggestion that the somatic cells of Crustacea change more readily in size when subjected to different temperatures (that is, that "Brook's Law" could be rephrased to imply a doubling of cell *number* between moults), but that eggs are affected in number rather than size. Presumably the effect of temperature is to limit the *potential* number of eggs produced. A female may bring forth only a reduced number of eggs if her immediate food supply is submarginal. This is suggested most clearly in the work of Davis (1961), who found that larger females of *Diaptomus* carried more eggs during some seasons, but at other times showed no such advantage. Several authors have speculated on the adaptive value of variations in clutch size. Clearly the manner in which the reproductive material is divided up is adaptive (amount of food for the developing young), but much of the intraspecific variability which has been studied carefully is the inescapable consequence of environmental variability. No work which fails to consider temperature during growth as a background to fecundity can be considered wholly reliable.

By good fortune there is much information on the fecundity of two animals whose size–temperature relationships have been established. These are representative of two phyla—the copepod (*Pseudocalanus minutus*) and the chaetognath (*Sagitta elegans*).

Not all copepods carry their eggs, but *P. minutus* carries a single bunch whose contents are easily counted. Marshall (1949) gave a very high correlation between median size of *P. minutus* females in Loch Striven and number of eggs in the bunch (given as $r = 0.98$, but calculated by me as 0.96). A logarithmic line fitted to her tabulated data (Fig. 10) has a higher correlation ($r = 0.975$). Study of a landlocked population in the Canadian arctic (McLaren, 1961) indicated that females produced only two successive clutches, regardless of the amount of food available for immediate utilization. It is possible that two clutches result from a shortage of males following initial fertilization (see Jacobs,

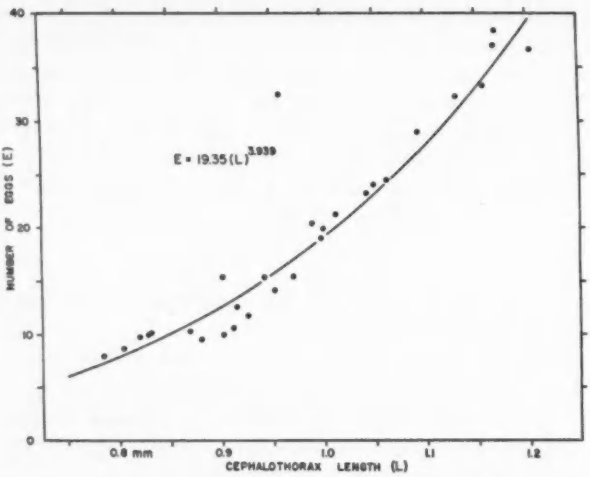

FIG. 10. Relationship between mean length of female *Pseudocalanus minutus* in Loch Striven and number of eggs carried in the egg bunch. The aberrant (open) point near top centre is excluded from calculation. Data from Marshall (1949).

1961), but it seems safe to conclude that twice the number of eggs shown in Fig. 10 will give a reasonable estimate of the fecundity of a female of any given length.

Russell (1932a) related ovary length to body length of "stage III" (adult) *S. elegans*. His tabulated results prove rather complex, for the relation is almost isogonic (double logarithmic slope = 1) between body lengths of about 10 and 14 mm, but heterogonic (slope ≠ 1) among smaller and larger animals. This is all the more curious, since Dunbar (1940) found that ovaries of arctic *S. elegans* grew persistently in strict heterogonic relationship (with a marked slope of about 3.85) from their appearance in young stages through full maturation. Although Russell does not give information on seasons or circumstances from which he collected his samples, it appears that his material included inviduals of "stage III" whose ovaries had not reached their full length for that stage. Figure 11 compares Russell's measurements with those of *S. elegans* from Ungava Bay and from Ogac Lake, a warm, landlocked arctic fiord (McLaren, 1961). The slope of ovary *growth* from Dunbar (1940) can equally well be applied to small and large animals from Russell's samples, and appears to justify the drawing by eye of a line relating *full size* of ovaries to body size of all populations. This line has a much smaller slope than that of growth. It remains only to convert ovary length into egg number. Assuming that the size of released eggs does not vary through the range of this species, the relationship between fully developed ovary length and egg number from arctic populations (Fig. 12) should apply throughout the range of this animal. I have found that even fully developed ovaries contain small eggs, and whether these mature as the larger eggs are

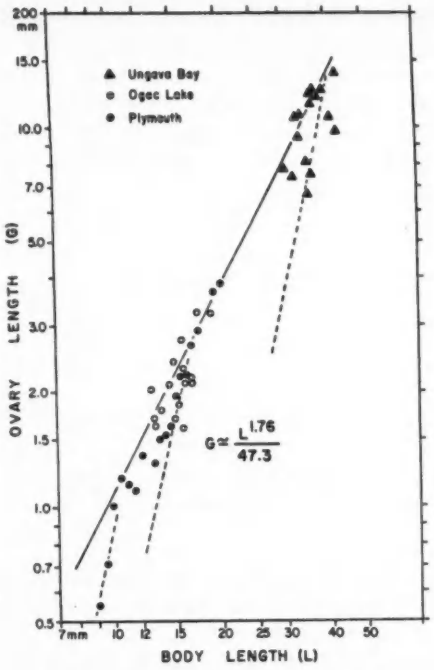

FIG. 11. Relationship of ovary length to body length of *Sagitta elegans* from Plymouth (Russell, 1932a) and from the Canadian arctic. The dashed line leading to the Ungava Bay specimens is for ovary *growth* from Dunbar (1940), and parallel lines are drawn for smaller ovaries. The solid line is fitted by eye to represent *full size* of ovaries from all populations.

released, or whether they are "nurse" cells is not finally answerable. However, all eggs are counted in the relationship of Fig. 12. Thus the number of eggs produced by a female grown at a given temperature off Plymouth can be determined from Fig. 7, 11 and 12, or by a derived formula.

Since these two species, and the majority of zooplankters, are semelparous (breeding once per lifetime—Cole, 1954), their population dynamics are very much simplified. In this paper we will be concerned with potential rates of increase as a measure of adaptive value. Rates of increase may be calculated over any time interval, but it is convenient to express them as the instantaneous coefficient of increase, the intrinsic rate of increase of the ecologist. For a semelparous species this is given by:

$$r = \frac{1}{D} \cdot \log_e (S \cdot E) \qquad \ldots\ldots(3)$$

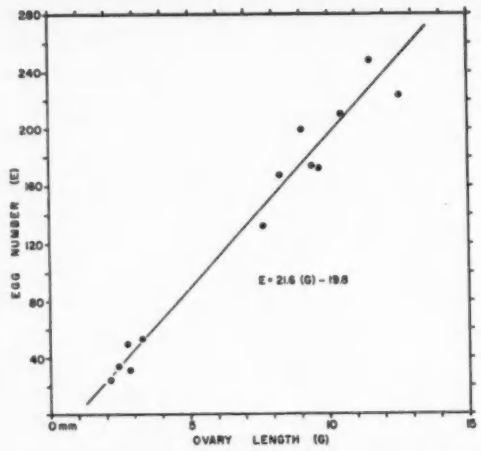

FIG. 12. Relationship between ovary length and number of eggs of *Sagitta elegans* from the Canadian arctic.

where E is the number of eggs produced, S is the proportion of eggs which survive to reproducing adults, D is the length of a generation and r the intrinsic rate of increase calculated on the basis of the same time unit (Cole, 1954). Such things as predation mortality might be greater in slow developing populations. On the other hand, "physiological" mortality may be a positive function of development rate, and therefore of temperature (see Taylor, 1960; Holt, 1960). The two effects may tend to cancel out. Presuming for the present that survival rate is the same, then the relative intrinsic rate of increase can be expressed as a function of egg number and generation length, and therefore as a function of temperature. This is best demonstrated by the examples of *Pseudocalanus minutus* and *Sagitta elegans*.

Unfortunately there are no direct observations of generation length as a function of temperature for either of these species. However, if we assume that the exponent of Bělehrádek's function for development rate is around 1.5 (cf. Fig. 1 and 2) and that the biological zero for development is the same as for size (compare Fig. 1b and 5), then we may approximate the relative length of generations at different temperatures. Food shortage may slow down development rate, and we are therefore justified in taking the shortest observed generation lengths as "real", temperature-dependent lengths. For *P. minutus* in Long Island Sound, evidence is given by Deevey (1956) that generation length was perhaps slightly less than one month, say 25 days, in December 1953, when mean temperature was about 7°C. Development may have been even more rapid later, but is not possible to determine. From Russell's data shown on Fig. 8, the most rapid development of *S. elegans* occurred at a time when the temperature was about 11.5°C, when the generation length again was about 0.8 month, or 25 days. Thus for these two species it is possible to convert relative

generation lengths into absolute generation lengths for any temperature, although the method cannot pretend to be very accurate. From such data on the numbers of generations per month and numbers of eggs per generation, the relative intrinsic rates of increase (on a monthly basis, assuming no mortality) are depicted as functions of temperature on Fig. 13 and 14. The numerical results are of course dependent on certain arbitrary choices of parameters, such as the value of the

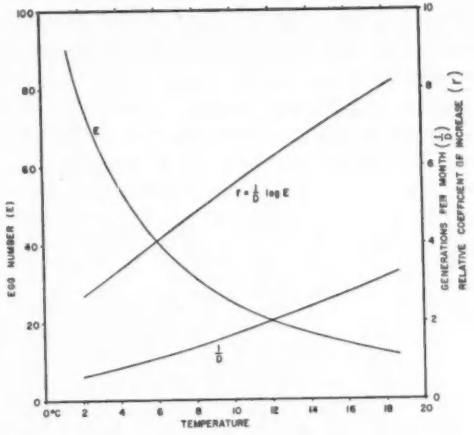

FIG. 13. Relative coefficient of rate of increase (assuming no mortality) of *Pseudocalanus minutus* as a function of temperature in Long Island Sound.

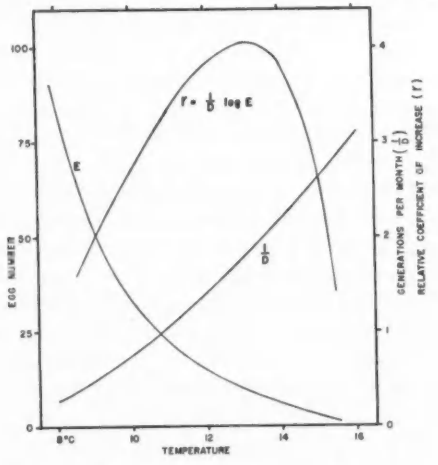

FIG. 14. Relative coefficient of rate of increase (assuming no mortality) of *Sagitta elegans* as a function of temperature off Plymouth.

exponent for Bělehrádek's function in generation lengths. However, the general form of relationship would be the same for any reasonable choice of parameters. *P. minutus* exhibits increasing r with rise of temperature within the range to which it is adapted in Long Island Sound, whereas a marked optimum is found in *S. elegans* of Plymouth. The latter result is due to a severe reduction of egg number at high temperatures; in fact, Russell (1932a) believed that reproduction ceased altogether at temperatures higher than about 14°C. The analysis here shows that this effect need not be regarded as a result of some sort of damage at high temperatures, but as a consequence of monotonic relations between physiological rates and temperature.

It should be pointed out that the reasoning presented above can be applied to males as well. Bisexual zooplankters, such as *S. elegans*, and males of unisexual ones, such as *P. minutus*, produce spermatophores which they attach to the females. It is not known how many spermatophores may be produced, but Marshall and Orr (1955a) quote evidence that they are quite few in *Calanus*, for example. Their number and rate of production will almost certainly be affected by the metabolic history of the animal.

It thus appears that *P. minutus*, all other things being equal, will benefit most at higher temperatures, presumably up to those levels where biochemical inactivation occurs. *S. elegans* should, from what has been said, avoid the higher temperatures within its vital range, perhaps by leaving surface waters when they are warmest. *S. elegans*, in which the ovary virtually disappears at high temperatures, is probably not typical, since most animals, like *P. minutus*, have a palpable if reduced number of eggs when they mature as small adults. At first glance there does not seem to be a general advantage in spending part of the time in cooler waters, as might be done by a vertical migrant. The next sections will attempt to show that thermal stratification is central to the adaptive value of vertical migration.

THE ADAPTIVE VALUE OF VERTICAL MIGRATION

The Value of Diurnal Migration Deduced from a Growth–Temperature Model

It is axiomatic that a population tends to be adapted to the prevailing selective forces of the environment. Conceivably an animal which only occurs in the plankton for a very small part of the year because of competitive advantages, for example, might have its metabolism narrowly adjusted to promote maximum rate of increase at the conditions of food and temperature which recur annually at that time. However, any animal that lives and reproduces in a variable environment falls prey to the fact that optimum conditions of food and temperature are probably never found together in either space or time.

Directly or indirectly the zooplankton depends on plant production in the illuminated surface waters, but it is these same surface waters which are almost universally warmer. It has been pointed out that the increased egg number, which an animal might gain by spending part of its time in deeper, colder water, is offset by retarded development. However, this reasoning has been based on

the assumption that breeding may occur at any time, and we must consider first the possibility of interrupted or seasonal reproduction. If successful reproduction is seasonally restricted by physical or biotic factors, then animals may be able to sacrifice considerable speed of development to secure greater ultimate fecundity. This is most simply understood in forms with an annual cycle, such as some macroplankters and almost all fish (and probably therefore many members of the migratory "deep scattering layer"). In these forms survival (S in Formula 3) could become a complicated negative function of development rate (D), since rapid development may be accompanied by prematurity and untimely reproduction. However, many zooplankters (including *Pseudocalanus minutus* and *Sagitta elegans*) are known to migrate in thermally stratified waters at times when generation follows upon generation, and when rate of increase, expressed as a function of development rate and fecundity alone, would appear to put migrants at a disadvantage.

The theory to be presented here depends first of all on the assumption that migrants, at least during certain seasons, can do all necessary feeding when near the surface. This seems to be tacitly assumed by many writers on the subject, probably because of observations (e.g. Gauld, 1953; Petipa, 1958) that migrants in fact do most if not all of their feeding when near the surface. The many published experiments on zooplankton grazing do not appear to have been designed to answer such questions satisfactorily. By increasing food density, several authors have demonstrated reductions or asymptotes in filtering rate (e.g. Ryther, 1954), ingestion rate (e.g. Marshall and Orr, 1955b), and assimilation rate (e.g. Richman, 1958). Short-term experiments (Rigler, 1961) on *Daphnia* have shown that ingestion rate may be regulated instantaneously, yet other experiments (Monakov and Sorokin, 1960) demonstrated that assimilation was constant above certain food levels in experiments lasting a few hours, while filtration rate was regulated or not, according to the kind of food (bacteria and algae). Observations have also been made (e.g. Gauld, 1953) that copepods may swim through suspensions of food cells without feeding at all. It seems curious that more attention has not been paid to the difference between instantaneous regulation of the daily assimilation rate, and regulation by fulfillment of "hunger" (as shown by Ivlev, 1960, for fishes). The difference is vital to the construction of general models of grazing and production, such as that of Cushing (1959), which would be badly distorted if animals were assumed not to be feeding for 24 hours a day. In this paper it will be assumed that migrant zooplankton, like the generality of animals, do not feed constantly, and can fill all their daily nutritional needs when nearer the surface if food is sufficiently rich.

It has been shown that development rate and full adult size can be expressed as functions of temperature alone when food is sufficiently abundant. What we have to consider when vertical migration is carried out in thermally stratified waters are the *consequences of feeding at temperatures which average higher than the temperatures governing growth and development* (assuming them to be continuous). Qualitatively this can be understood as giving an energy bonus through the more

efficient uptake of food at higher temperatures, together with the more efficient directing of energy to growth at lower temperatures. We are interested in how much this energy bonus might be, and whether it can be directed into fecundity in such a way as to overcome the retardation by low temperatures, and thus give migrants an advantage over individuals which spend their whole lives in the warmer surface waters.

In the analysis which follows, use will be made of a theoretical model which may appear dubious to some readers and unnecessary to others. However, there does not appear to be any other way of approaching the question analytically. Also, when the model is supplied with parameters independently derived from our considerations of temperature and growth, it has certain consequences which match observations about vertical migration which will be given later (p. 711 *et seq.*). To this extent I believe that the model, even if far from exact, gives some insight into the mechanism of vertical migration as a device for enhancing the rate of increase in thermally stratified waters.

The well-known equations of von Bertalanffy (e.g. 1957) have served as a starting point in many discussions of growth of animals. There is recent precedent for the use of these equations in analysing the effects of temperature on length of life and maximum size (Taylor, 1958, 1959, 1960). Taylor's conclusions depend on theoretically chosen constants in von Bertalanffy's equations, which have been disputed by other authors, and he has used a semilogarithmic temperature function, which cannot describe the empirical data in this paper (see Appendix). Certain other criticisms have been levelled by Holt (1959), who nonetheless acknowledges the general value of Taylor's new approaches. Since the effect of temperature on length of life and maximum size has been estimated directly in the present paper, it is possible to use von Bertalanffy's notions on growth in a far more general way.[2]

Von Bertalanffy says in the widest sense that growth of an animal must be the resultant of input ("anabolism") and output ("catabolism"); i.e.:

$$\frac{dW}{dt} = A - K \qquad \ldots\ldots(4a)$$

where W is the mass of the animal (other measures of growth could be substituted), and A and K are anabolism and catabolism per unit time in the same units. This much is undeniable. Further, anabolism and catabolism can always be expressed as functions of mass, so that:

$$\frac{dW}{dt} = a \cdot f(W) - k \cdot g(W) \qquad \ldots\ldots(4b)$$

where a and k are coefficients of anabolism and catabolism in units of mass per unit mass respectively. For animals in which growth rate decreases in time, and perforce when growth ceases altogether:

$$\frac{d\ f(W)}{d\ g(W)} < 1 \qquad \ldots\ldots(5)$$

[2]In his last paper, published posthumously after the present paper went to press, Taylor (1962) generalized the von Bertalanffy growth equation in the manner shown here.

Arguing from certain physiological evidence, von Bertalanffy assumes that catabolism is mass dependent and anabolism surface dependent, so that $g(W) = W$ and $f(W) = W^{\frac{2}{3}}$, which leads to ready solutions. Von Bertalanffy's interpretation of the form of these functions can be disputed (e.g. Ricker, 1958), and Richards (1959) has accordingly generalized this equation of limited growth for empirical use and shown it to be isomorphic with some other growth equations by removing theoretical restrictions on the parameters. In doing so he has retained the exponential character which von Bertalanffy assumed for f(W) and g(W), but has allowed a and k in Formula 4b to take on negative values, considering the theory to be based on "dubiously relevant metabolic studies". However, it must be stressed that these restrictions on parameters follow, not from experimental evidence, but from the definitions of anabolism and catabolism in Formulas 4a and 4b. If better empirical fits to examples of limited growth are obtained by allowing a or k to be negative (and Formula 5 unsatisfied), then this must be due to data error, or to the assumption that a and k are constants over the whole growth period, or to the wrong choice of f(W) and g(W), which of course may not even be analytical functions. Von Bertalanffy's argument that f(W) and g(W) might be given as $W^{\frac{2}{3}}$ and W respectively was based partly on widely accepted demonstrations that physiological rates are exponential functions of size, but there is little evidence that these particular exponents are universal (see, for example, the variety of exponents in Zeuthen, 1953). Even if we assume (cf. Parker and Larkin, 1959) that such exponents are characteristic only of a given stage (in this case full grown), even if growth is heterogonic, and even if we ignore von Bertalanffy's equation as a description of growth, it is possible (given Formula 4a) to define the mass W_∞ of an animal which has stopped growing in the presence of adequate food as:

$$W_\infty = \frac{W_\infty^x \, a}{W_\infty^y \, k} \ (x, y \text{ constant})$$

from which:

$$L_\infty^z = m \frac{a}{k} \qquad \ldots\ldots(6)$$

where L_∞ is the final length, m and z are constants, and a and k are physiologically determined coefficients of anabolism and catabolism (rates of input and output per unit mass of the animal).

Some zooplankters which go through successive moults after maturation (e.g. *Daphnia*) have been shown to have limited growth in the laboratory. Others (such as copepods) must at least approach asymptotic size, if something like Brook's Law holds, and stages are of successively longer duration. In fact, from everything that has been said about the relation between adult size and fecundity in semelparous species (pp. 698–701), it would appear that final size is set by a balance of anabolism and catabolism, since any excess input which is not "burned up" must appear as more growth or greater fecundity, which do not occur. If an animal reaches different *equilibrium* sizes at different temperatures, regardless of the mechanism this must reflect the fact that anabolism and catab-

olism are different functions of temperature as well as different functions of size. Let us consider that a and k in Formula 6 are related to temperature by Bělehrádek's functions with the same biological zero; then we may write:

$$L_\infty^z = m\frac{c_1(T+\alpha)_1^{b_1}}{c_2(T+\alpha)_2^{b_2}} = c\frac{(T+\alpha)_1^{b_1}}{(T+\alpha)_2^{b_2}} \quad \ldots\ldots(7a)$$

from which:

$$L_\infty^z = c(T+\alpha)_3^{b_3} \quad \ldots\ldots(7b)$$

Length cannot be considered a physiological rate as such, but since we have shown that final length is well described by Bělehrádek's function, we can say that length to any power will be given by this function of temperature (requiring only a change of exponent). This is emprical support for Formula 7b, and therefore suggests the validity of our premises (Formula 6) about the determination of asymptotic size as a function of physiological rates.

This general formula, describing equilibrium size as a function of temperature-dependent rates of input and output, is useful for the very question we have asked: what are the consequences of assimilating food (the sole source of input) at temperatures which average higher than those which determine catabolic ouput? To do this we may rewrite Formula 7a as:

$$L_\infty^z = c\frac{(T+\alpha)_1^{b_1}}{[(T-\beta)+\alpha]_2^{b_2}} \quad \ldots\ldots(8)$$

where β is the extent to which temperatures average lower during catabolism. When β is small, the error of assuming linearity (arithmetic mean) is negligible.

We have determined empirically that:

$$L_\infty = c(T+\alpha)^b$$

from which we can calculate Formula 7b and therefore 7a for any chosen values of b_2 and z, satisfying the given values of length by changes of c. There seem to be fairly definite restrictions on our choice of constants. To account for limited growth, $z>0$, and to match observations that physiological rates are related to mass by exponents of 1 or less, $z \lesssim 3$. Similarly, near-linear relations of physiological rates to temperature are known, but probably b_2 will not often exceed 3; the highest I have noted are those for early development of *Lophius americanus* eggs, well fitted by $D = 1.15\,(T+4)^{-3.7}$ hours, and commented on as being unusual by Berrill (1929).

Within such wide limits we may calculate the increase of length for any value of β from Formula 8. Assuming energy to be partitioned in the same way by migrants, we may express length as egg number by Formula 2. If development rate is independently related to temperature (but probably with comparable restrictions on the exponent) we may determine the relative advantage in rate of increase accruing from different values of β at different temperature levels. Actually, it is unlikely that growth and development can be considered as independent variables. If change in stage of development reflects a fixed relative growth increment (cf. Brook's Law), then solutions of the von Bertalanffy

equations (including the more general form implied by Formulas 8–10), show that rate of development will be proportional to the coefficient of catabolism k, which is a measure of relative rate of approach to the size asymptote. Further, catabolism in the operational sense given by von Bertalanffy is reflected, at least partly, in activities like respiration (also excretion, ecdysis, etc.), and there are demonstrations that development rates and such physiological rates may have comparable temperature characteristics (e.g. MacArthur and Baillie, 1929). All in all, it is likely, although not necessary for the arguments here, that b_2 in Formula 8 and the corresponding exponent in the function relating development rate to temperature will close if not identical in size.

Two examples of our "model" animals, *Pseudocalanus minutus* and *Sagitta elegans*, are given in Fig. 15 and 16. In these illustrations I have assumed that b_2 and the exponent of development rate are both equal to 1.5 (a rough mean of

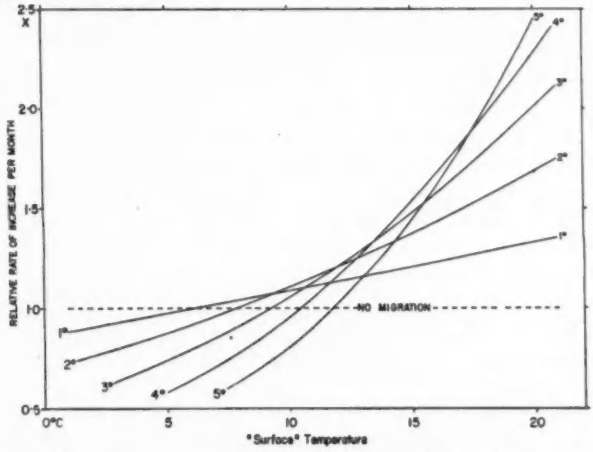

FIG. 15. A representative solution of the effects of vertical migration by *Pseudocalanus minutus* from Long Island Sound in thermally stratified waters. Each curve represents the relative rate of increase per month when mean temperature for uptake of food ("anabolism") is higher by the stated amount than mean temperature of "catabolic" processes. The monthly rates of increase are expressed relative to those of non-migrants, in which "anabolism" and "catabolism" are assumed to take place at the same "surface" temperatures.

those in Fig. 2 and 3) and that the ordinary von Bertalanffy equation of maximum size ($z = 1$) applies. Although the resulting curves are unlikely to be very close to reality, they are *representative* of a wide range of possible assumptions. It is possible to make the following general deductions from our model of an animal securing all necessary food in warm surface waters. In some cases (as when z in Formula 10 is large and b_2 much smaller than the exponent relating development to temperature) we can deduce no advantage to spending time in cooler depths, and in other cases there is an invariable advantage within the natural range of surface temperatures. The advantage, if any, increases with

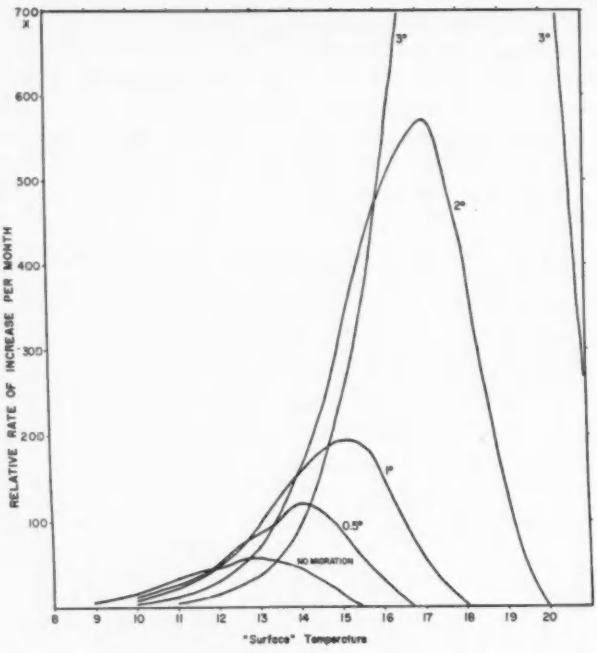

FIG. 16. A representative solution of the effects of vertical migration by *Sagitta elegans* from Plymouth in thermally stratified waters. Each curve represents the rate of increase per month which results from maintaining the stated differential between mean temperature of "anabolism" (at the "surface") and "catabolism".

temperature of the surface waters. *Within the most probable range of solutions, for animals securing all necessary food in surface waters, the model predicts that, vertical migration in thermally stratified waters will be disadvantageous at low surface temperatures, advantageous if not too extensive at intermediate surface temperatures, and that increasingly extensive migrations will be valuable as surface temperatures increase.*

There are many conflicting and confusing observations in the literature on vertical migration, and any theory, including the present one, would be badly strained in accounting for them all. The adaptive system suggested here is a complex one, in which an activity is controlled by one response (to light), modified by others (temperature, food), in order to adjust two rates (growth and development) to maximize the rate of increase. The mean vertical position, amplitude of migration, times of ascent and descent, and response to environmental differences which have proved most suitable for one stage, generation, locality, or season, will not necessarily be suitable for another stage, generation, locality, or season. The inertia of the genetically controlled parts of this system will ensure a considerable and confusing polymorphism. Nevertheless, there are patterns in the observations which agree with the present theory.

Observations on Effects of Food and Temperature

An arhythmical migration, controlled by food and temperature conditions, might be thought most advantageous. However, since there is no means available to zooplankton for detection of optimum conditions at a distance, it is not surprising that a rhythmical, light-controlled migration has been developed. It is also not surprising that feeding occurs in the dark and "resting" by day, since this would certainly give added benefits of escape from predation. According to the present theory, the extent of the migration and the response to light will ultimately be determined by the selective advantages of increased fecundity on the one hand, opposed by the disadvantages of retardation of development and metabolic drains of the migration itself. Although light is the necessary controlling basis of diurnal migration, this response could only be of adaptive value if other pertinent environmental factors modify and limit the migration.

In the first place it is necessary that migrants seek the warmest possible water, but only if the stratum also contains an adequate food supply; such strata may be quite thin, and not necessarily at the surface (see Sorokin, 1960). It has long been known that animals are more positively phototactic when they are starved (e.g. Clarke, 1932), and there are recent suggestions that copepods move upward more strongly when food is abundant in experimental settings (Bainbridge, 1953). These facts suggest that animals in nature may have a mechanism which enables them to continue to rise towards the warmer surface as long as they have not yet "found" food, or as long as it continues to be sufficient.

Observations on the effects of temperature are most significant. Dice (1914), and others since, have shown that certain cladocerans and copepods are more positively phototactic in cold waters; this is in accord with deductions in this paper that vertical migration would be disadvantageous. Zooplankters may or may not penetrate thermoclines when these are present (e.g. Hansen, 1951; Lacroix, 1961), even although the temperature differences involved are within the seasonal range of the species; this too seems to match deductions that small temperature differentials may at times be more advantageous than large. However, the most common class of observations of the effect of temperature is implicit in seasonal changes in the behaviour of migrants. There are times when zooplankters appear in large numbers near the surface during daytime, contrary to their "normal" habits of descent, summarized for numbers of marine species by Bigelow (1926) and for *Calanus* in detail by Marshall and Orr (1955a). It is significant that these observations are almost always made in late winter and early summer, when food is likely to be abundant and surface temperatures low to moderate. Later they begin vertical migration, and at the height of the hydrographic summer, they are found deep during the day, and migrate surfacewards only at dusk or night. (The animals may cease migration altogether and stay in the depths, but this phenomenon will be considered separately below—p. 716.) Such observations are in complete accord with deductions from growth-temperature relations that vertical migration would be disadvantageous when surface waters were relatively cool, and increasingly advantageous as surface waters warmed up, and do not seem explicable in any other terms.

Latitudinal Variations

It has become increasingly clear in recent years that there are broad latitudinal differences in the migratory behaviour of zooplankton, especially in the sea. These differences seem to conform well with predictions from the present theory.

The absence of vertical migration during periods of 24-hour daylight in the arctic (Bogorov, 1946) seemed to support the view that light is of controlling importance. Recently Digby (1961) has presented a more refined study of vertical distribution in two regions of Spitsbergen, where the diurnal variation in surface light intensity was only some 4- to 20-fold during his stay. Although he stresses the limited tendency of some species to be nearer the surface under cloud cover, what appears most striking is the very slight migration, if any, and the extraordinarily shallow depth preference of the animals studied. The maxima of numbers of *Calanus* almost always lay at 10 m or shallower, and most often at 1 m, and *Sagitta* were generally commonest at 5 m, and only once below 15 m. This distribution would be matched in midsummer in temperate waters at dusk or night, but certainly not during daylight hours. Arctic waters, with their narrow seasonal temperature range, may not as a rule reach temperatures at which migration becomes advantageous, and are usually almost unstratified. It is perhaps significant that Digby noted slightly more vertical movement in the quieter, more stratified of the two regions studied. Digby interpreted this to mean that any tendency to migrate was overcome by turbulence in the region with negligible stratification. Considering the swimming powers shown by many vertical migrants, it seems likely that the more static depth distribution was in response to the lack of thermal stratification.

Tropical seas are characterized by a narrow seasonal range of temperature at the surface, by a relatively deep isothermal layer of water through the year, and by more even seasonal distribution of primary production. For a migrant prepared to migrate through a long column of water, the advantages of alternating from depths of low temperature to depths of continuously adequate food are substantial. Thus it is not surprising to find that large and energetic forms such as euphausids and chaetognaths are conspicuous migrants of tropical waters and that small forms whose mean vertical position is near the surface show less tendency to migrate (Moore, 1949). Detailed studies of vertical migrations of a large number of tropical Pacific copepods have recently been made by Heinrich (1961), who showed that these animals have a much smaller tendency to migrate than their temperate counterparts. Most of the species which are non-migratory live, not at the surface, but between 25 and 100 m. Heinrich suggests that the greater depth of the euphotic zone in tropical waters permits copepods to feed at these levels. To his argument might be added the fact that these depths are even more isothermal during the year.

Tropical lakes, like the upper waters of the seas, tend to mix irregularly and develop little thermal stratification. We might expect vertical migration to be less pronounced, and this seems generally true, but the few available studies deserve closer attention. In the deep Lake Victoria, Worthington (1931)

demonstrated distinct diurnal migrations among cladocerans and copepods. At the time of his study (although probably not always thus), a thermal differential of 1–1.5°C was maintained during the 24 hours between the surface and 33 m, below which few migrants ventured. Migration was studied in three smaller west African lakes by Worthington and Ricardo (1936). Lake Naivisha, the shallowest, developed a thermal stratification of about 3° during the day in the upper 3 m, but was unstratified by night. Here a species of *Moina* and a *Cyclops* performed a normal migration *from on or near the bottom by day* towards the surface at night. Other species staying in the water column performed little or no migration. In the deeper Lake Bunyoni, with a temperature difference of about 1.5° between the surface and 35 m, at least during the day, only a species of *Cyclops* showed any noticeable migration, again from on or near the bottom. In the deepest and warmest lake, Lake Rudolph, which was little stratified on the day of observations, the only animal showing any pronounced diurnal change was a reverse migrant! *Diaptomus banforanus* ascended by day and descended by night. I know of no other example; the other supposed cases of reverse migration cited by these authors are simply of daytime accumulations near the surface at some seasons (see above, p. 711).

These observations seem to form a pattern to which the present theory can be extended, albeit speculatively. 1. If thermal stratification is a regular feature of the tropical lake (and the theory permits it to be very slight—see Fig. 15) then vertical migration of the ordinary sort could be valuable. 2. If migrants can reach and rest at the bottom, then this itself may offer energy conserving opportunities analagous to low temperatures. The phenomenon is also known in temperate lakes, where it could serve the same function. (In this connection it is worth noting that Woodmansee and Grantham (1961) have recently described a marked migration of *Cyclops* and *Chaoborus* in a small but strongly stratified lake in Mississippi. Here migrants spent the day in *deoxygenated* water, which might have had an energy conserving effect even greater than the slightly lower temperatures found there.) 3. In tropical lakes where surface waters are regularly and strongly heated and stratified during the day and mixed and cooled by night, a reversed migration could be adaptive.

Vertical migration has been most studied and seems most marked in temperate lakes and seas. It is in precisely these waters, with their wide seasonal range of temperature and strong tendency to stratify thermally, that the adaptive value of migration should be greatest, according to the theory given here. However, tropical and polar waters may be very revealing, and deserve more study.

Non-migratory "Epiplankton"

Some animals in boreal seas show little or no diurnal migration, although they live in waters where the advantages of such behaviour would seem large. They are mostly small animals which, together with the young stages of more migratory species, live near the surface and constitute the "epiplankton" of Bogorov's (1948) classification (a term unfortunately also applied to sessile organisms on zooplankters). The widespread and abundant copepods *Oithona similis* and *Paracalanus parvus* are representative members of the epiplankton,

and are among the smallest copepods. They have a wide thermal tolerance, and may breed throughout the year in many regions. How is it that these animals, subjected to what appear to be strong selective pressures, have such a limited tendency to migrate?

In the first place, the small size of most of the surface-dwelling species means that a given extent of migration would be proportionately more energy consuming. Small size probably also means greater predation, since small animals are vulnerable to the numerous young of predators. If animals continue to be preyed upon at a high rate throughout their lives, then any retarding effect of low temperature will entail proportionately higher mortality. Under these conditions, a rapid development could be selected for.

There are hints in the literature that the epiplankton have another feature in common. At least some, including the above-named copepods, may be found throughout the year, but have their seasonal maximum at times when net-diatoms are scarce. *Oithona* spp. and certain other small forms increase markedly in sewage-rich Norwegian fiords (Wiborg, 1944), but although they may feed on bacteria or detritus, they are probably adapted to feeding on the nannoplankton. This has been found in temperate marine waters to consist largely of tiny diatoms, whose biomass and sustained production exceed those of the net-phytoplankton at the surface (Yentsch and Ryther, 1959). It is possible that the small size of epiplankton is adapted to feeding on these tiny plants at the surface. I would like to speculate further that the epiplankton will be found to spend more time filtering their fine prey and, unlike migrants, unable to secure their daily nutritional needs by feeding only part of the day. In either case, the value of vertical migration would be constrained.

The temperature coefficients of anabolism and catabolism are themselves presumably under adaptive control. Increasing the difference between the coefficients (b_1 and b_2 in Formula 7a) will increase the effect of temperature on size, and on fecundity, and reduce the effect of temperature on intrinsic rate of increase. However, the primary value of increasing the difference between these exponents may be the advantage offered to vertical migrants. An animal forced for any reason to live near the surface at all times of year might well benefit by reducing the effect of temperature. It is interesting to note that size and egg number of the common epiplanktonic copepod, *Oithona similis*, show a much smaller seasonal range than found in known migratory copepods. The seasonal mean size of female *Calanus finmarchicus* may vary by some 30%, of *Pseudocalanus minutus* by about 50%, but of *Oithona similis* only by about 15%. The egg number carried by *O. similis* varies seasonally by three-fold, compared with five-fold in *P. minutus* (Marshall, 1949).

The marine epiplankton has its freshwater counterpart, which similarly thrives in surface waters after diatom flowerings of spring. McNaught and Hasler (1961) showed that the surface-dwelling *Daphnia* spp. of Lake Mendota in fact go through a small (1 m or less) diurnal migration. It is hard to see any adaptive value in such a migration, but it is also hard to see any energetic disadvantage in moving through a short water column which must be isothermal

and comparable in food supply throughout. It is possible that this migration is vestigial, and that it will be found in other "non-migratory" epiplankton. It may be evolutionarily easier to reduce the amplitude of migration than to dispense altogether with what may be a genetically conservative response to light.

Non-migratory Young Stages

It has been observed in a wide variety of forms that younger stages live near the surface and tend to be less migratory, or even altogether static in their vertical distribution. There are several possible explanations of this, all consistent with the theory developed in this paper.

In the first place, the young are as a rule produced in conditions of food appropriate to the species, but there is much evidence in the literature that the young are less efficient at securing food, less resistent to food shortages, and may suffer in interspecific competition (see Conover, 1956). Possibly the young are obliged to spend more time feeding, although Petipa (1958) has shown that all stages of *Acartia clausi* have a diurnal feeding rhythm, the younger more by day, and the older by night.

Mortality rates of young animals, for example nauplii, are greater, and presumably result in part from larger predation by young predators. For the same reasons mentioned in connection with the non-migratory "epiplankton", the accelerating effect of high surface temperatures may be important.

To me the most likely explanation is based on observations that the commencement of vertical migration is related to gametogenesis. Since a major morphological break occurs between the naupliar and copepodite stages of copepods, it might be expected that vertical migration would begin with this transition. In fact, vertical migration begins later, at around stage III copepodite in *Pseudocalanus minutus* and stage IV in *Calanus*, for example. These copepodite stages are in each species one prior to the stages at which secondary sexual characters become evident. Another example, *Sagitta elegans*, is said by many authors to exist mainly as "small", "young" or "immature" individuals in the surface waters, without reference to gonadial development. One author (Kramp, 1939) tabulates information on *S. elegans* from Greenland in August (when the waters were thermally stratified) which shows a distinct descent from the surface in all stages except "juveniles"—defined as those without any visible gonads.

Final size may be affected by temperature throughout life, and fecundity is most easily expressed as a function of final size. However it is to be understood that development rate, size and fecundity are affected by temperature through the partitioning of energy within the animal. It may be that future fecundity is not served by temperature advantages prior to a certain stage in the development of the gonads. On the other hand, advantages for fecundity may continue after "growth" (length increase) ceases. It is easily imagined that the partitioning of energy that occurs between moults of younger copepods occurs after the last moult to adulthood, and that fecundity is affected up to the end. It is of interest finally to note that Marshall and Orr (1960) have recently added the state of the gonad of adult *Calanus* to the factors which influence (or are influenced by ?) vertical migration in this species.

Seasonal Migrations

It is characteristic of many species of zooplankton to become deeper in their daytime vertical position as the season progresses. Since this behaviour as a rule takes them from increasingly warm surface waters through increasingly large temperature differentials in their migrations, it is in excellent accord with predictions from the growth–temperature model. However, many species descend to deep water at certain times of year, forego vertical migration altogether, and later ascend to the surface to give rise to a new generation or successive generations of diurnal migrants. When the pattern is this regular it is referred to in the literature as a seasonal migration. Often the descent and ascent occur at specific stages of development, and constitute a so-called ontogenetic migration. The ascent to the surface is often termed a breeding migration. All seem to be different names for essentially the same phenomenon. From many observations we may choose some typical ones from our "model" animal, *Pseudocalanus minutus*.

In temperate localities *P. minutus* may go through a succession of migratory generations before descending to overwinter, but at high latitudes the cycle is simpler. For example, in the Norwegian Sea (Østvedt, 1955) this copepod is annual, spawning at the time of the diatom maximum in April–May. The younger stages develop thereafter near the surface, but coincidentally with development to older copepodite stages, they abandon the surface waters. By August almost the entire population is found below 600 m, at which depth there is a sharp break in the temperature curve. Thus the animals spend the winter at below-zero temperatures, some 7–8° colder than the surface waters at *any* season. The animals overwinter largely as stage V copepodites, moulting to adults during the ascent in March–April, referred to by Østvedt as a spawning migration.

Bainbridge (1961) considers the so-called seasonal and ontogenetic migrations to be "mere variations imposed on the theme of diurnal vertical migration". I agree, and feel that such migrations have meaning in terms of the theory given in this paper. It is often suggested that the descended, non-migrant animals are conserving their energy in the cool depths, and certain species are even referred to as "hibernating" by some authors. Marshall and Orr (1955a) object that sometimes these deep waters are warmest in winter, but it should be stressed that the descent in well-documented cases occurs, not during the hydrographic winter, but at the end of the season of high biological production when surface waters may be at their warmest, while the ascent occurs when surface waters are cool and production high. Where the productive season is markedly seasonal, the dangers of poor timing seem obvious. Copepods, for example, which continue to live near the surface after the major plant production of spring and summer is finished, might achieve maturity, accelerated by warm temperatures and reproduce on ephemeral phytoplankton flowerings, but the number of their offspring would be small, and their fate in doubt. The selective advantage would lie with those animals which *retard* maturity by seeking the cold depths A further advantage would be that ultimately size and fecundity are increased

at the low temperatures, especially in animals whose development can continue slowly through utilization of stored food. Extreme cases of retardation, whose adaptive value is undoubted, are shown by species of rotifers, cladocerans and copepods with resting eggs. Intermediate between descent to the depths and formation of resting eggs are interesting examples of resting stages (perhaps diapaused) shown by some species of freshwater copepods (see Elgmork, 1959).

Migration and the "Fat Cycle"

In deducing the value of diurnal vertical migration from the effects of temperature on growth, it was assumed that the "bonus" of assimilated energy was apportioned in the same way by migrants in thermally stratified waters as by animals living at different constant temperatures. This might be expected to be true when reproduction was immediately advantageous, on the principle succinctly stated by Slobodkin (1961b) "that animals in general stay as lean as possible". However, at some times of year, especially when seasonal descent becomes necessary, animals may have to depend on a considerable reserve of stored food (e.g. the "oil gland" of copepods). A number of authors have noted that such reserves begin to build up in older, migratory stages prior to the seasonal descent. Still others (e.g. Marshall, 1949) have shown that animals of the descending stage which remain longest at the surface during the season of descent have less stored food. Some authors (e.g. Sushkina, 1962) have suggested that such energetic reserves are necessary before diurnal migration can be carried out. From everything that has been said, it is much more likely that the reverse is true, and that vertical migration is involved in building up these reserves through providing an energy bonus.

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REFERENCES

Allee, W. C., A. E. Emerson, O. Park, T. Park and K. P. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia. 837 pp.

Bainbridge, R. 1961. Migrations. Pages 431–463 *in* Volume 2 of The Physiology of Crustacea. T. H. Waterman, ed. Academic Press, New York.

1953. Studies on the interrelationships of zooplankton and phytoplankton. *J. Mar. Biol. Ass. U.K.*, **32**: 385–447.

Beklemishev, K. V. 1957. The spatial interrelationships of marine zoo- and phytoplankton. *Trudy Inst. Okeanol.*, **20**: 253–278. [English translation, Am. Inst. Biol. Sci., 1957.]

BĚLEHRÁDEK, J. 1935. Temperature and living matter. *Protoplasma Monograph.*, No. 8, 277 pp. Borntraeger, Berlin.
1957. Physiological aspects of heat and cold. *Ann. Rev. Physiol.*, **19**: 59–82.

BERRILL, N. J. 1929. The validity of *Lophius americanus* Val. as a species distinct from *L. piscatorius* Linn., with notes on rate of development. *Contr. Canadian Biol. Fish.*, N.S., **4**: 145–151.

BERTALANFFY, L. VON. 1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.*, **32**: 217–231.

BOGOROV, B. G. 1946. Peculiarities of diurnal vertical migrations of zooplankton in polar seas. *J. Mar. Res.*, **6**: 25–32.
1948. [Vertical distribution of zooplankton and vertical zonation of ocean waters.] *Trudy Inst. Okeanol.*, **2**:

BOOIJ, H. L., AND H. P. WOLVEKAMP. 1944. Catenary processes, master reactions and limiting factors. *Bibliotheca Biotheoretica*, **1**: 145–224.

CARSON, H. L. 1957. The species as a field for gene recombination. Pages 23–38 *in* The Species Problem. Ernst Mayr, ed. *Am. Ass. Adv. Sci., Publ.* No. 50.

CLARKE, G. L. 1936. On the depth at which fish can see. *Ecology*, **17**: 452–456.
1932. Quantitative aspects of the change of phototropic sign in *Daphnia*. *J. Expt. Biol.*, **9**: 180–211.

CLARKE, G. L., AND R. H. BACKUS. 1956. Measurements of light penetration in relation to vertical migration and records of luminescence of deep-sea animals. *Deep-Sea Res.*, **4**: 1–14.

COKER, R. E. 1933. Influence of temperature on size of freshwater copepods (*Cyclops*). *Int. Rev. Hydrobiol.*, **29**: 406–436.

COLE, L. C. 1954. The population consequences of life history phenomena. *Quart. Rev. Biol.*, **29**: 103–137.

CONOVER, R. C. 1956. Oceanography of Long Island Sound, 1952–54. VI. Biology of *Acartia clausi* and *A. tonsa*. *Bull. Bingham Oceanogr. Coll.*, **56**: 156–233.

CUSHING, D. H. 1959. On the nature of production in the sea. *U.K. Ministry Agric. and Fisheries, Fish. Invest.*, Ser. II, **22**(6), 40 pp.
1951. The vertical migration of planktonic Crustacea. *Biol. Reviews*, **26**: 158–192.

DAVID, P. M. 1961. The influence of vertical migration on speciation in the oceanic plankton. *Systematic Zool.*, **10**: 10–16.

DAVIS, C. C. 1959. Breeding of calanoid copepods in Lake Erie. *Verh. int. Ver. Limnol.*, **14**: 933–942.

DEEVEY, G. B. 1960. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bull. Bingham Ocean. Coll.*, **17**(2): 55–86.
1956. Oceanography of Long Island Sound, 1952–54. V. Zooplankton. *Ibid.*, **15**: 113–155.

DICE, L. R. 1914. The factors determining the vertical movement of *Daphnia*. *J. Anim. Behavior*, **4**: 229–265.

DIGBY, P. S. B. 1961. The vertical distribution and movement of marine plankton under midnight-sun conditions in Spitsbergen. *J. Anim. Ecol.*, **30**: 9–25.

DUNBAR, M. J. 1957. The determinants of production in northern seas: a study of the biology of *Themisto libellula* Mandt. *Canadian J. Zool.*, **35**: 797–819.
1940. On the size distribution and breeding cycles of four marine planktonic animals from the Arctic. *J. Anim. Ecol.*, **9**: 215–226.

EDMONDSON, W. T. 1960. Reproductive rates of rotifers in natural populations. *Mem. Ist. Italiano Idrobiol.*, **12**: 21–77.

ELGMORK, K. 1959. Seasonal occurrence of *Cyclops strenuus strenuus* in relation to environment in small water bodies in southern Norway. *Folia Limnol. Scandinavica*, No. 11, 195 pp.

EVANS, R. M., F. C. PURDIE AND C. P. HICKMAN JR. 1962. The effect of temperature and photoperiod on the respiratory metabolism of rainbow trout (*Salmo gairdneri*). *Canadian J. Zool.*, **40**: 107–118.

FLORKE, M., G. KEIZ AND G. WANGORSCH. 1954. Über die Temperatur- Stoffweschel- Relation und die Wärmeresistenz einiger Süsswasser-fische und der Flusskrebses. *Z. Fischere*, **3**: 241–310.

FRY, F. E. J. 1947. Effects of the environment on animal activity. *Publ. Ontario Fish. Res. Lab.*, No. 68, 62 pp.

GAULD, D. T. 1953. Diurnal variations in the grazing of planktonic copepods. *J. Mar. Biol. Ass. U.K.*, **31**: 461–474.

GREEN, J. 1956. Growth, size and reproduction in *Daphnia* (Crustacea: Cladocera). *Proc. Zool. Soc. London*, **126**: 173–204.

HANSEN, K. V. 1951. On the diurnal migration of zooplankton in relation to the discontinuity layer. *J. Cons. Explor. Mer*, **17**: 231–241.

HARDY, A. C. 1956. The open sea. Its natural history: the world of plankton. Collins, London. 335 pp.

HARDY, A. C., AND E. R. GUNTHER. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. *Discovery Rept.*, No. 11, 456 pp.

HARRIS, J. E. 1953. Physical factors involved in the vertical migration of zooplankton. *Quart. J. Microscop. Sci.*, **94**: 537–550.

HARVEY, H. W., L. H. N. COOPER, M. V. LEBOUR AND F. S. RUSSELL. 1935. Plankton production and its control. *J. Mar. Biol. Ass. U.K.*, **20**: 407–441.

HEINRICH, A. K. 1961. [On the vertical distribution of the copepods in the region to the southeast of Japan.] *Trudy Inst. Okeanol.*, **51**: 82–102.

HOLT, S. J. 1959. Water temperature and cod growth-rate. *J. Cons. Explor. Mer*, **24**: 374–376.

1960. Letter to the editor. *Ibid.*, **25**: 225–227.

HUTCHINSON, G. E. 1951. Copepodology for the ornithologist. *Ecology*, **32**: 527–577.

INGLE, L., T. R. WOOD AND A. M. BANTA. 1937. A study on the longevity, growth, reproduction and heart rate in *Daphnia longispina* as influenced by limitations in quantity of food. *J. Exp. Zool.*, **76**: 325–352.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven. 302 pp.

JACOBS, J. 1961. Laboratory cultivation of the marine copepod *Pseudodiaptomus coronatus* Williams. *Limnol. Oceanogr.*, **6**: 443–446.

JENSEN, J. P. 1958. The relation between body size and the number of eggs in marine malacostrakes. *Medd. Danmarks Fisk.-Havunders.*, Ny Ser., **2**(19), 25 pp.

JØRGENSEN, N. R. 1916. Undersøgelser over Frequensflader og Korrelation. Copenhagen. [Cited by Nielsen and Evans, 1960.]

KANWISHER, J. W. 1955. Freezing in intertidal animals. *Biol. Bull.*, **109**: 56–63.

1959. Histology and metabolism of frozen intertidal animals. *Ibid.*, **116**: 258–264.

KRAMP, P. L. 1939. The Godthaab Expedition 1928. Chaetognatha. *Medd. om Grønland*, **80**(5), 40 pp.

KRÜGER, F. 1961. Über den Exponenten der Temperaturfunktion biologischer Vorgänge und deren Grössenabhängigkeit. *Biol. Zentralblatt*, **80**: 721–750.

LACROIX, G. 1961. Les migrations verticales journalières des euphausides à l'entrée de la Baie des Chaleurs. *Naturaliste Canadien*, **53**: 257–316.

LOEB, J. 1908. Über den Temperaturkoeffizienten für die Lebensdauer Kaltblütiger Thiere und über die Ursache des naturliden Todes. *Arch. ges. Physiol.*, **124**: 411–426.

MACARTHUR, J. W., AND W. H. T. BAILLIE. 1929. Metabolic activity and duration of life. *J. Exp. Zool.*, **53**: 221–268.

MACKINTOSH, N. A. 1937. The seasonal circulation of the Antarctic macroplankton. *Discovery Rept.*, **16**: 365–412.

MCLAREN, I. A. MS, 1961. The hydrography and zooplankton of Ogac Lake, a landlocked fiord on Baffin Island. Ph.D. Thesis, Yale University.

MCNAUGHT, D. C., AND A. D. HASLER. 1961. Surface schooling and feeding behavior in the white bass, *Roccus chrysops* (Rafinesque), in Lake Mendota. *Limnol. Oceanogr.*, **6**: 53–60.

MANTEUFEL, B. P. 1959. [Adaptive significance of the periodic migrations of water organisms.] *Voprosy Ikhtiologii*, **13**: 3–15.

MARGALEF, R. 1955. Temperature and morphology in freshwater organisms. *Verh. int. Ver. Limnol.*, **12**: 507–514.

MARSHALL, S. M. 1949. On the biology of the small copepods in Loch Striven. *J. Mar. Biol. Ass. U.K.*, **28**: 45–122.

MARSHALL, S. M., A. G. NICHOLS AND A. P. ORR. 1934. On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. *J. Mar. Biol. Ass. U.K.*, **19**: 793–827.

MARSHALL, S. M., AND A. P. ORR. 1960. On the biology of *Calanus finmarchicus*. XI. Observations on vertical migration especially in female *Calanus*. *J. Mar. Biol. Ass. U.K.*, **39**: 135–147.

1955a. The biology of a marine copepod *Calanus finmarchicus* (Gunnerus). Oliver and Boyd, Edinburgh. 188 pp.

1955b. On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation, and excretion in adult and stage V *Calanus*. *J. Mar. Biol. Ass. U.K.*, **34**: 495–529.

1953. *Calanus finmarchicus:* Egg production and egg development in Tromsø Sound in spring. *Acta Borealia, A. Scientia*, No. 5, 21 pp.

MONAKOV, A. V., AND YU. I. SOROKIN. 1959. [An experimental investigation of *Daphnia* nutrition using C^{14}.] *Dokl. Akad. Nauk S.S.S.R.*, **135**: 1516–1518.

MOORE, H. B. 1949. The zooplankton of the upper waters of the Bermuda area of the north Atlantic. *Bull. Bingham Ocean. Coll.*, **12**(2), 97 pp.

MOORE, H. B., AND E. G. CORWIN. 1956. The effects of temperature, illumination and pressure on the vertical distribution of zooplankton. *Bull. Mar. Sci. Gulf Caribbean*, **10**: 430–443.

NIELSEN, E. T., AND D. G. EVANS. 1960. Duration of the pupal stage of *Aedes taeniorhynchus* with a discussion of the velocity of development as a function of temperature. *Oikos*, **11**: 200–222.

ØSTVEDT, O.-J. 1955. Zooplankton investigations from Weather Ship M in the Norwegian Sea, 1948–49. *Hvalrådets Skr.*, No. 40, 93 pp.

PARKER, R. R., AND P. A. LARKIN. 1959. A concept of growth in fishes. *J. Fish. Res. Bd. Canada*, **16**: 721–745.

PETIPA, T. S. 1958. [The diurnal feeding rhythm of the copepod *Acartia clausi*.] *Dokl. Akad. Nauk S.S.S.R.*, **120**: 191–192.

RAVERA, O., AND V. TONOLLI. 1956. Body size and number of eggs in diaptomids, as related to water renewal in mountain lakes. *Limnol. Oceanogr.*, **1**: 118–122.

RICHARDS, F. J. 1959. A flexible growth function for empirical use. *J. Expt. Bot.*, **10**: 290–300.

RICHMAN, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.*, **28**: 273–291.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

RIGLER, F. H. 1961. The relation between concentration of food and feeding rate of *Daphnia magna* Straus. *Canadian J. Zool.*, **39**: 857–868.

RILEY, G. A. 1956. Oceanography of Long Island Sound. II. Physical Oceanography. *Bull. Bingham Oceanogr. Coll.*, **15**: 15–46.

RUSSELL, F. S. 1932a. On the biology of Sagitta. The breeding and growth of *Sagitta elegans* Verrill in the Plymouth area, 1930–31. *J. Mar. Biol. Ass. U.K.*, **18**: 131–145.

1932b. On the biology of Sagitta. II. The breeding and growth of *Sagitta setosa* J. Müller in the Plymouth area, with a comparison with that of *S. elegans* Verrill. *Ibid.*, **18**: 147–160.

RYTHER, J. H. 1954. Inhibitory effects of phytoplankton on the feeding of *Daphnia magna*, with reference to growth, reproduction and survival. *Ecology*, **35**: 522–533.

SCHOLANDER, P. F., W. FLAGG, V. WALTERS AND L. IRVING. 1953a. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zoöl.*, **26**: 67–92.

SCHOLANDER, P. F., W. FLAGG, R. J. HOCK AND L. IRVING. 1953b. Studies on the physiology of frozen plants and animals in the arctic. *J. Cell. Comp. Physiol.*, **42**: (Suppl. 1), 56 pp.

SHAW, R. F., AND L. B. BEAUREGARD. 1962. Temperature and life span in poikilothermous animals. *Nature*, **196**: 454–457.

SLOBODKIN, L. B. 1961a. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York. 184 pp.

1961b. Preliminary ideas for a predictive theory of ecology. *Am. Natur.*, **45**: 147–153.

SOROKIN, J. I. 1960. Vertical distribution of phytoplankton and the primary organic production in the sea. *J. Cons. Explor. Mer*, **26**: 49–56.

STEELE, J. H. 1961. Primary production. Pages 519–538 *in* Oceanography. M. Sears, ed. *Am. Ass. Adv. Sci. Publ.*, No. 67.

SUSHKINA, A. P. 1962. [Rate of fat consumption at various temperatures and life cycle of *Calanus finmarchicus* (Gunn.) and *Calanus glacialis* Jaschn.] *Zool. Zhurnal*, **41**: 1004–1012.

TAYLOR, C. C. 1958. Cod growth and temperature. *J. Cons. Explor. Mer*, **23**: 366–370.

1959. Temperature and growth—the Pacific razor clam. *Ibid.*, **25**: 93–101.

1960. Temperature, growth, and mortality—the Pacific cockle. *Ibid.*, **26**: 117–124.

1962. Growth equations with metabolic parameters. *Ibid.*, **27**: 270–286.

TERAO, A., AND T. TANAKA. 1930. Duration of life in the water flea, *Moina macrocarpa* Strauss, in relation to temperature. *J. Imp. Fish. Inst.* (Tokyo), **25**: 67.

WATERMAN, T. H. 1960. Comment following paper by G. L. Clarke. *In* Symposium on radiant energy in the sea, ed. N. J. Jerlov. *Union Géodés. Géophys. Int., Monogr.*, No. 10, pp. 102–103.

WIBORG, K. F. 1944. The production of zooplankton in a landlocked fiord, the Nordåsvatn near Bergen, in 1941–42, with special reference to the copepods. *Rept. Norwegian Fish. Mar. Invest.*, **7**(7), 83 pp.

WINBERG, G. G. 1956. Rate of metabolism and food requirements of fishes. *Nauchnye Trudy Belorusskogo Gosud. Universit. V. I. Lenina*, Minsk, 253 pp. [FRB Translation Series No. 194]

WOODMANSEE, R. A. 1958. The seasonal distribution of the zooplankton off Chicken Key in Biscayne Bay, Florida. *Ecology*, **39**: 247–262.

WOODMANSEE, R. A., AND B. J. GRANTHAM. 1961. Diel vertical migrations of two zooplankters (*Mesocyclops* and *Chaoborus*) in a Mississippi lake. *Ecology*, **42**: 619–628.

WORTHINGTON, E. B. 1931. Vertical movements of fresh-water macroplankton. *Int. Rev. Hydrobiol.*, **25**: 394–436.

WORTHINGTON, E. B., AND C. K. RICARDO. 1936. Scientific results of the Cambridge expedition to the East African lakes, 1930–31, No. 17. The vertical distribution and movements of the plankton in Lakes Rudolf, Naivasha, Edward and Bunyoni. *J. Linnaean Soc. London*, **40**: 33–69.

WYNNE-EDWARDS, V. C. 1962. Animal dispersal in relation to social behaviour. Oliver and Boyd, Edinburgh, 653 pp.

YENTSCH, C. S., AND J. H. RYTHER. 1959. Relative significance of the net phytoplankton and nannoplankton in the waters of Vineyard Sound. *J. Cons. Explor. Mer*, **24**: 231–238.

ZEUTHEN, E. 1953. Oxygen uptake as related to body size in organisms. *Quart. Rev. Biol.*, **28**: 1–12.

APPENDIX. ON CHOOSING A TEMPERATURE FUNCTION

In this paper use has been made of an analytical function relating development rates and size to temperature. This formula, first used by Bělehrádek (1935), closely describes the data used in this paper, which were not chosen for the purpose of giving a good fit. This may be enough justification for its use, but the reader might ask if another formula would do as well. Mathematically, of course, a more complex polynomial equation could always be devised for any given example to account for the slightest deviation from a more general equation. However, I will confine this survey to expressions which have been used in physiology, and mostly to their empirical rather than theoretical aspects.

The much used Van't Hoff or Q_{10} rule suggests that physiological rate is often doubled or more for each 10° rise in temperature. When Q_{10} is constant the logarithm of the rate will be linearly related to temperature as

$$V = ab^T \qquad \ldots\ldots(A1)$$

where V is the velocity of the process, T the temperature in degrees Celsius, and a and b constants. This is an empirical approximation of theoretically sounder laws (of Arrhenius) which give a straight line relationship between the logarithm of rate of *chemical* reaction and the reciprocal of absolute temperature. Since the plot of the reciprocal of absolute temperature against temperature Celsius is virtually linear over the viable range of organisms, metabolic rates which have a constant Q_{10} might be thought to be following ordinary laws of chemical reaction. In fact, as physiologists have long known, Q_{10} often lies between 2 and 3 in mid-temperature ranges, but tends to decrease over the viable range of the animals being tested. In spite of this, the commonest temperature-metabolism plot in the literature continues to be semilogarithmic, and the departure from linearity is still the source of much discussion. Thus Scholander *et al.* (1953b) and Kanwisher (1955, 1959) describe the respiration of freeze-resistant animals well below 0°C. Respiration falls off rapidly at sub-zero temperatures on their semilogarithmic plot, and they ascribe this great increase of Q_{10} to the effects of freeze-drying or hypersalinity. The importance of these studies may not be that they reveal departures from a single metabolism–temperature relation, but that they extend this relation to levels unattainable in most animals. There is characteristically a distinct increase of Q_{10} at lower experimental temperatures, but animals as a rule die with much further reduction of temperature. This is shown clearly in the many examples of arctic *and* tropical Crustacea graphed by Scholander *et al.* (1953a). Other authors, recognizing that Q_{10} is not constant, have been forced to the mathematically clumsy device of discussing single metabolism–temperature curves in terms of variable coefficients. There is a marked compulsion for theorizing about deviations from a constant Q_{10}. The underlying chemical reactions are said to be "interlocking" in some undefined way, although it is not clear why this should preclude a rate-controlling reaction at any given temperature. Or, the process is supposed to involve replacement of the controlling ("master") reaction; that is, a succession of chemical processes with different coefficients. The unhappy complexity of such approaches is well shown in the monograph by Booij and Wolvekamp (1944).

The tenacious use of Q_{10} and the semilogarithmic plot can probably be traced to the relative simplicity in concept and calculation of this expression for rate of change, and the underlying belief that control must be simple and chemical. However, this has led to a certain blindness to its empirical inadequacy, and it certainly cannot be used to describe the material considered in this paper.

At the highest experimental temperatures it is often noted that metabolic rates increase less rapidly, or even decrease. This fact is the basis for several empirical expressions which have in common the use of maximum rate as a parameter. These formulas, which include the "catenary" of Janisch, the "logistic" used by Davidson and others, and a formula close to the expression for the Gaussian law of errors, applied by Pradhan, have been recently reviewed by Nielsen and Evans (1960). Most workers agree that very high temperatures are deleterious and destroy the very system being studied, but there is no theoretical reason to suppose that any of these formulas could account for this destruction, together with the stimulating effect of temperature. They also have the mathematical shortcoming that the maximum velocity is often hard to determine, and may not even be reached when very high temperatures are not used in experiments. At any rate, Nielsen and Evans show that the formulas must be rejected on empirical grounds. The logistic, for example, implies a mid-range inflection and upper asymptote (not peak) which are simply not universal features of experimental data. The present paper is concerned with temperatures in nature, and it must be said that metabolic or developmental rates are *as a rule* monotonically increasing functions of temperature within the natural temperature range. This is true of the data in this paper, and is reflected clearly in comparisons of eurythermic animals, such as the catfish *Ameiurus* depicted by Fry (1947), with stenothermic ones, such as the salmonid fishes, which are such frequent experimental subjects.

Some serious workers on fish metabolism, such as Fry (1947) and Winberg (1956), feel that no analytical function adequately describes the relationship with temperature. Fry and his co-workers are content to fit curves by eye, but Winberg has revived the belief of August Krogh, that temperature and respiration can be related by a general law, common to all groups. The law is a purely empirical one, expressed by what had come to be known as Krogh's "normal curve". It is assumed that each temperature level has a characteristic Q_{10}. Thus if values of respiration are expressed as percentages of respiration at 20°C, they are supposed to lie along the normal curve. Winberg showed by graphing material from some 18 species of fish that respiration conformed quite well to the normal curve, and used this curve as a standard in his study of fish metabolism. Whatever the merits of Krogh's normal curve as an empirical approximation in some cases, it cannot have general validity. In the first place it fails to account for the fact that respiration approaches the zero level at greatly different temperatures in different animals; see, for example, the comparison of tropical and arctic invertebrates in Scholander *et al.* (1953a). In the second place, it fails to describe the differences in curvature which are in fact found in metabolism–temperature data; some rates are virtually linear functions of temperature, while others are highly curvilinear.

As far as I am aware, three and only three monotonic functions have been used in physiology to account for differences in both origin and shape of temperature–metabolism curves. I will consider these in historical order.

Nielsen and Evans (1960) have compared the above and other functions fitted to data on insect development. In doing so they have revived an analytical generalization of Krogh's normal curve developed by Jørgensen (1916). Krogh's empirical curve has fixed parameters; Jørgensen found it expressed by the equation

$$V = c + ab^T \qquad \ldots\ldots(A2)$$

where V is the velocity of the process, T the temperature, and a, b, and c are constants. Nielsen and Evans show this "Krogh-Jørgensen function" to be a much closer fit to their data than any other function considered by them and plead convincingly for its general empirical validity in describing the accelerating effect of increasing temperature. They also account for the depressing effect of very high temperatures by application of the same function, using negative parameters, from an arbitrary point of origin near the upper experimental limits. This might equally well

be done with other formulas, but for reasons given above (p. 723), we are concerned here only with the monotonically increasing portion of curves, such as are usually revealed in nature. Nielsen and Evans stress that the Krogh-Jørgensen function is purely empirical, and cannot find any biological basis for its application. It might be noted that Formula (A2) actually resembles the Van't Hoff function (Formula A1, above) with the addition of a constant.

Next, we have to consider Bělehrádek's (1935) general empirical formula, with the form

$$V = a(T + \alpha)^b \qquad \ldots\ldots(A3)$$

where V is the velocity of the process, T the temperature, and a, b, and α constants. This is the development of an earlier equation by Bělehrádek which did not include the important scale correction, α. Many subsequent authors have applied and understandably dismissed this earlier function, but few have considered formula (A3), which was shown by Bělehrádek to give a very satisfactory fit to a wide variety of rates and organisms (see also his recent review, 1957).

Recently, Krüger (1961) has offered yet another general empirical function. In form, it is a modified Arrhenius function, which may be written:

$$V = \frac{a}{\frac{1}{b^{T+c}}} \qquad \ldots\ldots(A4)$$

where V is the velocity of the process, T the temperature, and a, b, and c are constants. Again, Krüger has shown this function to give a good expression of respiration of molluscs, plants, and fish at different temperatures.

Now the mathematical similarity of Formulas (A2), (A3) and (A4) should be noted. All are 3-parameter equations, with scale corrections for fixing origins, and exponentials, reciprocals, or both, for depicting slope changes. Such equations are bound to approximate many monotonically changing distributions over the viable temperature range. For example, Krogh's normal curve, which has been generalized in Formula (A2), is also very closely described between 0 and 30°C by:

$$V = a\,(T + 16)^{3.2}$$

as a special case of Formula (A3), and also by:

$$V = \frac{a}{\frac{1}{b^{T+42}}}$$

as a special case of Formula (A4). None of the three authors of these equations considered the two alternatives to his choice, but in fact any one of the three formulas can describe the same data about equally well. However, in choosing between equally accurate empirical formulas to describe biological material, it seems to me that other criteria should be considered. Conceptually simplest formulas should be chosen; one should avoid formulas which have purely mathematical restraints on the parameters, or unaccountable characteristics outside the domain of application; and, finally, one should choose formulas whose parameters reflect possible biological characteristics, even if these are not fully understood. Bělehrádek's function certainly fulfills these requirements better than the alternatives.

First of all, the parameter α in Formula (A3) is a scale correction which is called by Bělehrádek the "biological zero" of the process being studied. This concept is common to many areas of ecological and physiological discussion, and is often used by ecologists to correct an approximate linear (hyperbolic) relation between development and temperature (see discussion in Allee *et al.*, 1949). It subsumes observations that the whole curve of temperature response may be shifted, as between arctic and tropical species for example, and corrects for this in the direct and obvious way, unlike the scale corrections in Formulas (A2) and (A4). The biological zero may lie above or below zero Celsius, and death or "unphysiological" effects (see Fig. 2b in this paper) normally intervene at temperatures well above the biological zero. Death by freezing, for example, may or may not occur in animals which have comparable respiration rates at temperatures very close to freezing.

Formulas (A2) and (A4) can be considered to be modifications of the semi-logarithmic, "chemical" functions of Van't Hoff and Arrhenius, although the addition of scale corrections destroys their theoretical basis and renders them purely empirical. Formula (A3) implies that there will be a linear relation with slope b between log of the physiological rate and log of the corrected temperature. From observations that dehydration, like cold, depressed physiological rates, and that temperature affected viscosity and the diffusion of small particles in fluid media in a comparable, double-logarithmic fashion, Bělehrádek concluded that the rate-controlling factors in biological systems were not chemical, but physical. In this framework, $T-\alpha$ is the level at which intracellular motion ceases, equivalent to gelation in physical systems, and physiological rate is controlled at viable temperatures by something akin to viscosity coefficients. Possibly rates are depressed at very high temperatures by chemical denaturation of the enzyme systems, but it is worth noting that viscosity of living systems is increased at unnaturally high temperatures. In view of advances in cytology and demonstrations that energetic activities in the cell are carried out on supermolecular, particulate or structural systems, Bělehrádek's ideas certainly merit biophysical reconsideration.

After the discussion of various formulas which might be used, it remains to demonstrate the empirical superiority of Bělehrádek's function. Note that the Krogh-Jørgensen and Krüger functions are emprically equivalent, and that Bělehrádek's function has been chosen on other grounds. Note also that Krogh's normal curve is a special case of Bělehrádek's function, so that if the latter is fitted it will always be statistically more accurate than Krogh's curve.

Figure A1 depicts data on the development of sea urchin eggs from Loeb (1908), chosen because they are "classical", but otherwise typical of such studies. Loeb, like others since, wrote of the changing "temperature coefficients" (Q_{10}) throughout the experimental temperature range, a fact which is obvious from the fitted semilogarithmic line in Fig. A1. This clumsy means of describing the relation between development and temperature is completely overcome if Bělehrádek's function is used.

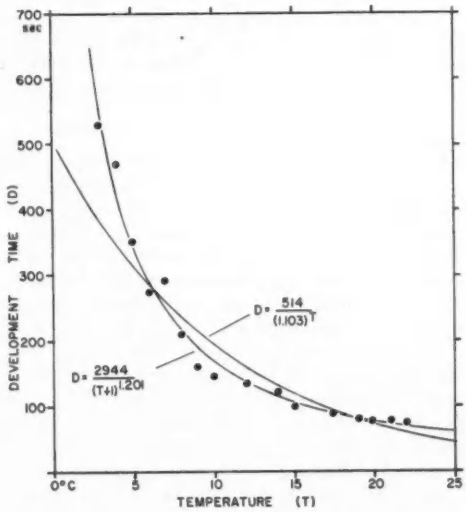

FIG. A1. Effect of temperature on time of development of sea urchin ova between fertilization and first cleavage. (Data from Loeb, 1908.)

Finally, certain restrictions on the use of this or any other analytical function should be noted. In the first place, as pointed out above, no simple function can be expected to cover deviations outside the natural temperature range of the organism. Further, even if such things as activity are controlled (as by Fry, 1947, and his co-workers, but not by students of zooplankton respiration), it may be too much to expect that this function will fit metabolic activities of whole organisms. This may be demonstrated by example. Figure A2 is typical of the great mass of published

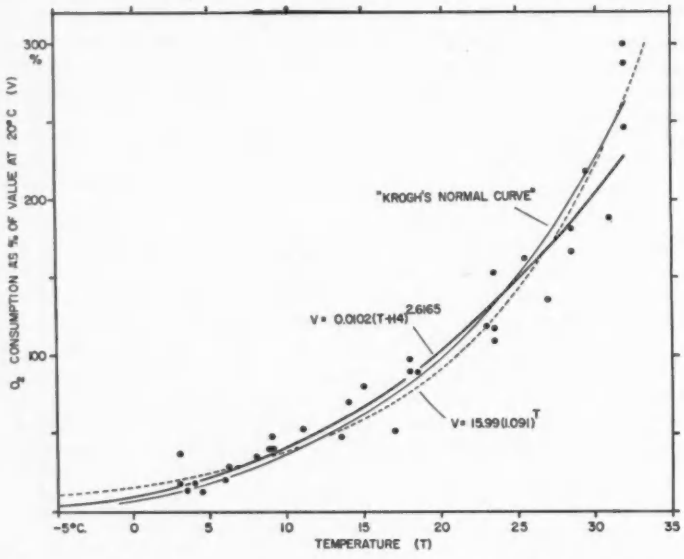

FIG. A2. Effect of temperature on respiration of the fish *Gambusia*. (After Winberg, 1956, who assumed the data to be well described by "Krogh's normal curve".)

experimental data on respiration and temperature, in that the amount of scatter is great. There seems to be little subjective reason for choosing among the three depicted temperature functions, although in fact the statistically closest fit is given by Bělehrádek's function. On the other hand, data in Fig. A3, relating oxygen consumption of excised gill of rainbow trout to temperature, are virtually perfectly described by this function. The whole organism consists of parts and tissues which may have quite different temperature characteristics and, further, there may be humoral effects. For example, Evans *et al.* (1962) show that, unlike the gill, the brain and liver of rainbow trout have higher respiration at 8° than at 16° (curiously referred to by these authors as "compensation", at low temperatures, although it is difficult to see how this differs from depression at high temperatures, in this stenothermic fish). Thus, what applies to gill could not apply to whole fish. Even if very accurate in depicting the physiological activity of individual tissues, a series of different exponential functions cannot be summated as a rate for the whole organism. It can be shown that Bělehrádek's function will be a good approximation if the parameters α and b in Formula (A3) are not too widely divergent in the rates for individual parts. Similarly development rates of different parts of an organism may have different temperature characteristics, but it is usual to classify stages of development in terms of events in a single system or organ (moult number, size of gonad, etc.). This may be part of the reason for the demonstrated empirical adequacy of Bělehrádek's function for development rate of "whole" organisms, although for a perfect fit α and b in Formula (A3) must also be invariant in time.

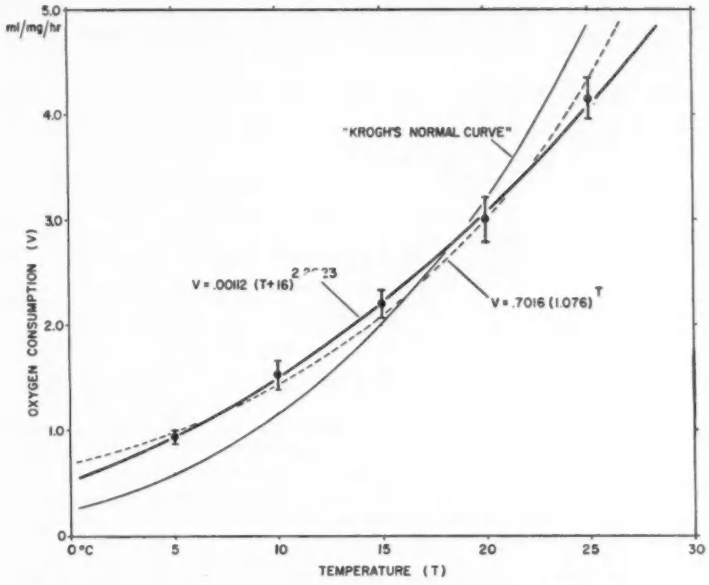

FIG. A3. Effect of temperature on oxygen consumption of excised gills of rainbow trout, *Salmo gairdneri* (means and two standard errors of means). From Florke *et al.* (1954).

I have fitted Bělehrádek's function to a wide variety of metabolic and developmental rates, and believe that it will be generally valid except where there are good reasons, of the sort discussed above, for not considering any analytical function. I think that this conceptually simple function, whose significant constants reflect two most obvious characteristics—scale position and curvilinearity—should supplant other analytical means of describing the metabolic response to temperature. In particular, the whole concept of Q_{10} should be abandoned, or at least confined to considerations of rate of change at different temperatures.

Amino Acid Composition of Representatives of Eight Bacterial Genera with Reference to Aquatic Productivity[1]

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ABSTRACT

Representatives of eight bacterial genera were grown under identical conditions and the harvested, washed cells were analyzed quantitatively for eighteen amino acids using chemical methods. All of the bacteria contained the eighteen amino acids and, although quantitative differences were noted, variation in composition was not great. Cell nitrogen content averaged 11.91% of the dry weight. Some of the nutritional implications of the data are discussed.

INTRODUCTION

The studies reviewed by Thatcher (1954) and Anderson and Jackson (1958) demonstrate that microorganisms can serve as an important source of animal food. These authors point out that the critical need in many parts of the world for food, particularly protein, and the economic advantages and efficiency of microbial elaboration of food and vitamins from inexpensive raw materials has spurred research into the composition of microorganisms. The evaluation of the nitrogen content of microorganisms, however, has been directed mainly toward furnishing data on which to base mammalian diets and, as a consequence, to some or all of the essential amino acids.

Several examples listed in the review of the nutrition of the protozoa by Johnson (1956) illustrate different and more extensive amino acid requirements. One strain of *Tetrahymena* has an absolute requirement for serine in addition to the ten essential amino acids; *Paramecium multimicronucleatum* has an absolute requirement for tyrosine, phenylalanine, tryptophan, methionine, threonine, isoleucine, leucine, histidine, valine, and serine and growth is reduced by the omission of lysine, arginine, proline, alanine, glutamic acid, aspartic acid, and glycine; *Glaucoma* is dependent on polypeptides but can utilize free amino acids of which aspartic is the most active; and *Colpidium* is inhibited by free amino acids singly and in various combinations. Interestingly, *Glaucoma*, *Tetrahymena*, and *Colpidium* are noted for their bacterial diet in nature.

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ZoBell and Feltham (1938), reporting on the ability of sea mussels, sand crabs, and Gephyrean worms to ingest and digest bacteria, cite the ability of bacteria to convert soluble and insoluble material to particulate, edible, cell substance without the use of radiant energy as a feature which makes bacteria important in marine nutrition. The list of animals which derive part or all of their food from the ingestion of bacteria includes protozoa, copepods, rotifers, ciliates, certain snails, nematodes, tube worms, and some crustacea; in fact all those who feed on mucus, or by filtering and burrowing (ZoBell, 1946). Galtsoff *et al.* (1937) published diets for many detritus feeders which are based wholly or in part on microorganisms.

Thus it becomes important to know the complete amino acid composition of bacteria for the assessment of their role in the natural nutrition of detritus feeders, and also to know the composition of one of the nutritional factors which can be and is manipulated in changing basic aquatic productivity. Additionally this information would provide dietary data for laboratory studies of animals who feed extensively on bacteria and themselves form an important link in the food chain in marine and fresh waters.

This study reports the results of the chemical determination of the amino acid composition of representatives of eight bacterial genera all grown in the same complete medium for the same period of time and provides data for the calculation of the cell protein content.

MATERIALS AND METHODS

Cultures for the study are listed in Table I and were obtained from this laboratory's culture collection (FRBC) and the American Type Culture Collection (ATCC). The medium used for growth of quantities of cells sufficient for analysis was: yeast extract (Difco-Bacto), 10 g; peptone, 5 g; dibasic potassium phosphate, 5 g; disodium ethylenediaminetetraacetate, 0.25 g; trace metals (Aaronson, 1955), 5 ml; distilled water, 960 ml; the pH was adjusted to 7.2, the medium autoclaved and, after cooling, 40 ml of a sterile 20% glucose solution was added aseptically. Cultures, transferred twice on agar slants at 24-hr intervals, were used to inoculate 50-ml quantities of the liquid growth medium dispensed in 250-ml Erlenmeyer flasks. The flasks were incubated at 25° C on a reciprocal shaker; after 24 hr, 0.5 ml was transferred to a second set of flasks and the procedure repeated. Ten ml of these cultures was added to each of two 2800-ml Fernbach flasks each containing 1000 ml of the same medium, shaken for 24 hr at 25° C on a gyrotory shaker, harvested, washed 4 times with 0.86% saline at 4° C and the packed cells stored at −25° C to await analysis. The moisture content was determined from the weight lost by preparations kept at 105° C for 24 hr, followed by 1 hr at room temperature in a vacuum dessicator with phosphorus pentoxide as the drying agent. Nitrogen was determined by the micro-Kjeldahl method using a selenium catalyst; cystine plus cysteine by the Winterstein-Folin reaction as adapted by Block and Bolling (1951) and tryptophan by the method of Spies and Chambers (1949). Other amino acids were determined by ion-exchange chromatography of acid hydrolysates of samples

TABLE I. Amino acid content of eight bacteria.

Determination	ORGANISMS																Average values	
	Aerobacter aerogenes FRBC 101		*Escherichia coli* FRBC 123		*Pseudomonas aeruginosa* FRBC 34		*Serratia marcescens* FRBC 138		*Achromobacter* sp. FRBC 176		*Micrococcus aureus* FRBC 190		*Sarcina lutea* FRBC 137		*Bacillus cereus* ATCC 10702			
	g/16 g N	Moles percent	g/16 g N	Moles percent	g/16 g N	Moles percent	g/16 g N	Moles percent	g/16 g N	Moles percent	g/16 g N	Moles percent	g/16 g N	Moles percent	g/16 g N	Moles percent	g/16 g N	Moles percent
Lysine	5.61	5.95	5.76	6.34	5.26	5.98	5.28	5.99	5.85	6.68	7.34	7.97	7.28	7.78	5.56	7.15	5.99	6.73
Histidine	1.92	1.92	1.66	1.72	1.86	2.09	1.79	1.93	1.81	1.95	1.31	1.33	1.45	1.47	1.44	1.75	1.66	1.75
Ammonia	2.00		1.95		2.10		2.16		2.41		1.94		2.38		2.49		2.18	
Arginine	5.90	5.25	5.65	5.23	5.89	5.62	5.25	4.98	5.22	5.00	4.63	4.22	4.80	4.31	3.84	4.15	5.15	4.85
Aspartic acid	8.56	9.97	8.09	9.78	7.44	9.29	8.06	10.06	8.28	10.38	5.80	6.91	4.94	5.79	5.42	7.64	7.07	8.72
Threonine*	4.06	5.28	4.18	5.65	3.64	5.09	3.74	5.21	3.88	5.44	3.48	4.64	3.40	4.45	3.08	4.86	3.68	5.07
Serine*	3.32	4.89	3.15	4.81	2.82	4.47	2.97	4.70	2.86	4.54	2.18	3.29	1.95	2.90	1.93	3.45	2.65	4.13
Glutamic acid	10.30	10.84	9.07	9.92	9.57	10.82	9.38	10.59	9.42	10.66	13.10	14.09	15.10	16.08	9.83	12.53	10.72	11.96
Proline	2.96	3.98	3.08	4.29	3.00	4.32	2.79	4.03	2.74	3.98	4.44	6.13	3.35	4.54	1.99	3.25	3.04	4.34
Glycine	4.91	10.11	5.01	10.73	4.70	10.41	4.62	10.23	4.67	10.40	4.52	9.56	5.97	12.43	3.45	8.63	4.73	10.34
Alanine	6.18	10.75	6.20	11.18	6.07	11.32	5.87	10.94	5.50	10.32	11.60	20.64	10.10	17.80	6.24	13.13	7.10	13.31
Cystine/2	0.74	0.96	0.35	0.46	0.44	0.61	0.41	0.56	0.55	0.81	0.68	0.90	0.59	0.77	0.58	0.90	0.54	0.74
Valine	5.54	7.32	5.31	7.28	5.24	7.43	5.35	7.57	5.30	7.56	4.29	5.83	4.22	5.58	4.18	6.70	4.93	6.90
Methionine	2.45	2.54	2.49	2.69	2.22	2.48	2.52	2.81	2.01	2.26	1.61	1.71	1.29	1.36	4.27	5.37	2.36	2.59
Isoleucine	4.09	4.83	4.20	5.15	3.52	4.45	3.76	4.75	3.92	5.01	2.32	2.81	2.25	2.67	3.14	4.50	3.40	4.25
Leucine	6.90	8.15	6.00	7.37	6.95	8.81	6.49	8.22	6.33	8.07	4.28	5.18	4.62	5.50	4.51	6.46	5.76	7.21
Tyrosine	3.51	3.00	2.86	2.54	2.64	2.43	3.07	2.81	2.63	2.43	2.15	1.89	4.52	3.90	3.39	3.51	3.10	2.80
Phenylalanine	3.41	3.21	3.79	3.70	3.46	3.47	3.64	3.67	3.37	3.41	2.34	2.25	1.97	1.86	4.73	5.37	3.34	3.32
Tryptophan	1.38	1.05	1.46	1.16	1.20	0.98	1.18	0.96	1.29	1.05	0.81	0.64	1.03	0.78	0.74	0.68	1.14	0.91
Nitrogen percent of dry weight	10.82		13.92		12.90		12.0		11.86		10.83		10.73		12.23		11.91	
Nitrogen recovery percent	81.9		78.9		78.1		77.4		78.3		78.4		81.9		70.5		78.17	

*Corrected for hydrolytic loss.

using a Beckman-Spinco Automatic Amino Acid Analyzer (Spackman *et al.*, 1958; Spackman, 1960). Hydrolysis was accomplished by refluxing 1.0 g of sample (wet weight) for 24 hr with 25 ml constant boiling hydrochloric acid which was then diluted to 50.0 ml. Excess acid was removed from a 5.0 ml aliquot by distillation under reduced pressure (repeated three times after addition of water). The residue was taken up in citrate buffer pH 2.2 ("sample-diluent" buffer containing thiodiglycol, BRIJ, and octanoic acid, (Spackman, 1960)), and brought to the volume required to give a nitrogen concentration of 0.300 mg/ml and filtered through sintered glass to remove humin (Horn *et al.*, 1953). One ml of the filtrate was used for ion-exchange chromatography. The values for threonine and serine were corrected for hydrolytic loss by applying the factors 1.10 and 1.07 respectively (Hoogland *et al.*, 1961). The other amino acids did not require corrections.

RESULTS AND DISCUSSION

The cells of eight bacteria have been analyzed quantitatively for eighteen amino acids and the data summarized in Table I. While it is realized that not all the nitrogen in the cells is part of the cell protein, the percentage of nitrogen is given to permit an approximation of cell protein and the calculation of the concentration of the amino acids per g of dried cells. The amino acid content of the cells has been reported as "g amino acid per 16 g nitrogen", thus following established procedure and allowing easy comparison with similar work. Additionally, this data has been calculated and presented as "moles percent" to permit a comparison on a molecular basis and to be more meaningful for dietary planning and nutritional work, since biologically the amino acids are assimilated and used on a molecular basis. The average values are given in terms of both "g amino acid per 16 g nitrogen" and "moles percent". Cystine and cysteine are reported collectively as half cystine (cystine/2).

The average value of cell nitrogen for the eight bacteria was 11.91% of dry weight which compares favourably with the value of 11.1% given by Anderson and Jackson (1958). It should be remembered that this value represents only the nitrogen provided by the amino, imino and amide groups; since the micro-Kjeldahl technique does not measure nitro, azo or other ring forms of nitrogen the true value for cell nitrogen should be somewhat higher. The average nitrogen recovery value of 78.18% indicates that there are nitrogen compounds other than purines, pyrimidines, and the reported amino acids still to be determined.

The average moles percent values of the amino acids in the cells, listed in decreasing order of abundance, are: alanine, 13.31; glutamic acid, 11.96; glycine, 10.34; aspartic acid, 8.72; leucine: 7.21; valine, 6.90; lysine, 6.73; threonine, 5.07; arginine, 4.85; proline, 4.34; isoleucine, 4.25; serine, 4.13; phenylalanine, 3.32; tyrosine, 2.80; methionine, 2.59; histidine, 1.75; tryptophan, 0.91; and cystine/2, 0.74. Comparison with the analyses performed on *Escherichia coli* by Roberts *et al.* (1955) shows a slightly different order, but the differences are extremely small except for cysteine which is reported as 1.7 moles percent versus an average of 0.74 in this paper. The essential amino acids, with the exception of tryptophan,

agree quite well with the values for bacteria reported by Anderson *et al.* (1958) and Reusser *et al.* (1957). Their average values for tryptophan are 0.3 and 3.9 g per 16 g N, respectively, while the average value in this study is 1.14, approximately halfway between the values in these two reports. Rao and Wadhwani (1956) point out in their report on *Mycobacterium tuberculosis* that differences are to be expected due to differences in the age of cultures and nature of the nitrogen source. However, in keeping with the findings of Stokes and Gunness (1946), the amino acid compositions of the organisms are qualitatively similar with remarkably small quantitative differences. The results of this investigation indicate that the amino acid composition of the cells cannot be used as a basis for classification of bacteria.

Micrococcus aureus is significantly lower than the other bacteria in total aromatic amino acids, phenylalanine plus tyrosine, having approximately two thirds the average value of 6.12 moles percent while the value for *Bacillus cereus* is one third higher than the average. *Micrococcus aureus*, *Sarcina lutea*, and *Bacillus cereus* possess the greatest quantities of lysine, the amino acid most often deficient in diets based on cereal grains. Wheat, for example, is poor in lysine, averaging 2.5 g/16 g N, while bovine liver contains 6.1 g/16 g N (Block and Weiss, 1956), approximately the same average values as that given for bacteria in this study.

Anderson and Jackson (1958) state that diets based on cereal grains and forage field crops require amino acid supplements and suggest that amino acids supplied in protein form, e.g., microorganisms, are used much more economically in the animal body than those supplied in the free state. This study shows that bacteria, which carry their amino acids largely in the protein form, are rich enough in the essential amino acids to supplement mammalian diets and complete enough in the others to meet the extensive requirements of the protozoa and other animals who can and do feed on bacteria. The possibilities inherent in this type of food production terrestially have been emphasized by Thaysen (1943) but little attention has been given to the aquatic environment. This report is intended to supply background information for studies in this direction.

REFERENCES

AARONSON, S. 1955. The purine requirements of *Staphylococcus flavocyaneus*. *J. Gen. Microbiol.*, **12**: 147–155.

ANDERSON, R. F., AND R. W. JACKSON. 1958. Essential amino acids in microbial proteins. *Appl. Microbiol.*, **6**: 369–373.

ANDERSON, R. F., R. A. RHODES, G. E. N. NELSON, M. C. SHEKLETON, A. BARRETO AND M. ARNOLD. 1958. Lysine, methionine, and tryptophan content of microorganisms. I. Bacteria. *J. Bacteriol.*, **76**: 131–135.

BLOCK, R. J., AND D. BOLLING. 1951. The amino acid composition of proteins and foods, analytical methods and results. Charles C. Thomas, Springfield, Illinois, 2nd ed., pp. 195–196.

BLOCK, R. J., AND K. W. WEISS. 1956. Amino Acid Handbook: methods and results of protein analysis. Charles C. Thomas, Springfield, Illinois.

GALTSOFF, P. S., F. E. LUTZ, P. S. WELCH AND J. G. NEEDHAM. 1937. Culture methods for invertebrate animals. Comstock, New York, N.Y.

HOOGLAND, P. L., H. C. FREEMAN, B. TRUSCOTT AND A. E. J. WADDELL. 1961. The amino acid composition of cod tropomyosin. *J. Fish. Res. Bd. Canada*, **18**: 501–512.

HORN, N. J., A. E. BLUM, C. E. F. GERSDORFF AND H. W. WARREN. 1953. Sources of error in microbiological determinations of amino acids on acid hydrolysates. I. Effect of humin on amino acid values. *J. Biol. Chem.*, **203**: 907–913.

JOHNSON, W. H. 1956. Nutrition of protozoa. *Ann. Rev. Microbiol.*, **10**: 193–212.

RAO, N. A. N., AND T. K. WADHWANI. 1956. The amino acid composition of the cellular protein of *Mycobacterium tuberculosis*. *J. Bacteriol.*, **76**: 12–15.

ROBERTS, R. B., D. B. COWIE, P. H. ABELSON, E. T. BOLTON AND R. J. BRITTEN. 1955. Studies of biosynthesis in *Escherichia coli*. Carnegie Inst. Wash. Publ. 607.

REUSSER, F., J. F. T. SPENCER AND H. R. SALLANS. 1957. Essential amino acids in microorganisms. *Canadian J. Microbiol.*, **3**: 721–728.

SPACKMAN, D. H. 1960. Instruction manual and handbook Beckman/Spinco Amino Acid Analyzer. Spinco Div., Beckman Instruments, Inc., Palo Alto, California.

SPACKMAN, D. H., W. H. STEIN AND S. MOORE. 1958. Automatic recording apparatus for use in the chromatography of amino acids. *Anal. Chem.*, **30**: 1190–1206.

SPIES, J. R., AND D. C. CHAMBERS. 1949. Chemical determination of tryptophan in proteins. *Anal. Chem.*, **21**: 1249–1266.

STOKES, J. L., AND M. GUNNESS. 1946. The amino acid composition of microorganisms. *J. Bacteriol.*, **52**: 195–207.

THATCHER, F. S. 1954. Foods and feeds from fungi. *Ann. Rev. Microbiol.*, **8**: 449–472.

THAYSEN, A. C. 1943. Value of microorganisms in nutrition (food yeast). *Nature*, **151**: 406–408.

ZOBELL, C. E. 1946. Marine Microbiology. Chronica Botanica Co., Waltham, Massachusetts, pp. 173–175.

ZOBELL, C. E., AND C. B. FELTHAM. 1938. Bacteria as food for certain marine invertebrates. *J. Marine Res.*, **1**: 312–327.

The Spatial Distribution of Fish in Gill Nets[1]

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ABSTRACT

The spatial distribution of yellow perch (*Perca flavescens*), white sucker (*Catostomus commersoni*), smelt (*Osmerus mordax*), chub spp. (*Coregonus* spp.) and alewife (*Alosa pseudoharengus*) caught in gill nets fished in South Bay of Lake Huron is described. The vertical distribution was essentially the same for all catches examined, the fish being concentrated towards the bottom of the net. The lateral distribution varied with species, mesh size and setting. Three types of lateral distribution were recognized, namely random, dispersed and bunched. Possible reasons for these different types and the relation between the distribution of fish in the net and in the water are discussed.

INTRODUCTION

The interpretation of catches of fish taken in gill nets is complicated by the passive nature of this type of fishing gear. Moyle (1950) cites the following factors as affecting gill-net catches: the movement of the fish, shape and structure of the fish, and the associative pattern or grouping of the individuals of any species or assemblage of species. This paper is concerned with the last-named factor.

Maeda (1953) analysed the distribution of salmon in gill nets fished off the Aleutian Islands and found intraspecific differences in both the vertical and lateral aspects. By dividing the nets into shallow, middle and deep portions by eye and counting the numbers of fish in each, he found that the maximum concentration of *Oncorhynchus gorbuscha* occurred at a slightly deeper level than did *O. kisutch*, *O. nerka* or *O. keta*. In analysing the lateral distribution he counted the numbers of fish in successive segments along the net, determined their frequency distribution and compared it with the Poisson, Thomas and Polya-Eggenberger distributions by chi-square tests. The lateral distribution of *O. nerka* proved to be random while those for the other species belonged to one or other of the contagious types, i.e. Thomas' or Polya-Eggenberger's.

In the present study catches of a gang of experimental gill nets fished in South Bay of Lake Huron (45° 37.0′ N, 81° 54.0′ W) are analysed to determine the spatial distribution of various species in the nets. Species studied are the yellow perch (*Perca flavescens*), white sucker (*Catostomus commersoni*), smelt (*Osmerus mordax*,) chub spp. (*Coregonus* spp.) and the alewife (*Alosa pseudoharengus*).

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DESCRIPTION OF GEAR AND SAMPLING METHOD

The gang of gill nets consisted of 12 nylon nets of mesh sizes varying from 1 to 5 inches (25–127 mm) stretched measure (between every second knot). All nets were hung on the half and the specifications as to thread sizes, mesh sizes and depths of web were those given by McCombie and Fry (1960).

For the first lift, the nets of 1.75-inch (44-mm) mesh and smaller were 50 yards (46 m) in length and the nets of 2-inch (51-mm) mesh and over were 150 yards (137 m). Thereafter all nets in the gang were 50 yards long. For each set all sections in the gang were located in approximately the same depth of water. The first set was made in relatively shallow water (5–6 fathoms, 9–11 m) and succeeding sets were made in deeper water, up to 25 fathoms (46 m).

The nets were brought to the laboratory with the fish still entangled in the web and then stretched over sheets of plywood which had been marked off in a grid of 1-foot squares. As each fish was taken from the net, its position in the net was recorded on a paper grid corresponding to the grid on the plywood. The records for each species and for each net in the gang were kept separate.

RESULTS

Table I shows the numbers of fish of each species caught in successive mesh sizes at each setting. Altogether 1623 fish were captured. Most of these were taken in mesh sizes from 1 to 2.25 inches. Only the suckers and a few smelt were caught in meshes larger than 2.75 inches. The latter were caught by the teeth.

Vertical Distribution of Fish in the Nets

The vertical distribution of the fish observed in the 4 settings was sufficiently similar to justify pooling the data for all settings. The number of specimens of each species was totalled for each 1-foot depth-interval of netting. The total for each interval was then converted into a percentage of the grand total for the species (Fig. 1). All species were concentrated towards the bottom of the net.

However, there is a notable difference between the vertical distribution of the suckers, smelt, chubs and alewife and that of the perch. For the first 4 species about 88% of the fish were caught in the first 3 feet (91 cm) of the net above the bottom and the maximum concentration was between the 1- and 2-foot levels. In contrast, about 80% of the perch were caught within the first foot (30 cm) above the lead line.

It is surprising that the sucker, a bottom feeder, was taken in greatest numbers some distance from the bottom. Evidently the position of the fish in the net may bear no relation to its feeding habits.

The concentration of the perch in the bottom foot of the gill nets is consistent with nocturnal behaviour of this species as observed by Hasler and Villemonte (1953) in Lake Mendota. Using echo-sounder traces and direct observations by divers, these authors found that "the schools of perch moved onto the Second Point shelf high over the bottom during their pre-sundown, inshore movement

TABLE I. Summary of gill net catches of yellow perch, white suckers, chub spp., smelt and alewives.

Fishing period	Depth of set (Fath. m)	Species	Total catches in each mesh size (inches) of net gang											
			1	1.5	1.75	2	2.25	2.5	2.75	3	3.5	4	4.5	5
July 13–14	5–6 9–11	Perch	3	164	142	38	8	13	–	–	–	–	–	–
		Sucker	–	–	2	6	18	11	14	10	90	11	2	3
		Alewife	10	442	25	2	–	3	–	–	–	–	–	–
August 4–5	10 18	Perch	–	17	43	33	13	–	–	–	–	–	–	–
		Smelt	27	1	3	4	3	5	–	–	–	–	–	–
		Alewife	–	28	5	–	–	–	–	–	–	–	–	–
August 6–7	20 37	Chub spp.	–	10	27	7	–	1	1	–	–	–	–	–
		Smelt	113	9	5	9	3	14	8	2	2	3	2	3
August 7–8	25 46	Chub spp.	–	–	40	27	4	1	–	–	–	–	–	–
		Smelt	114	4	4	3	3	1	2	–	–	2	–	–

and reached their greatest concentration during the hour before sunset. They settled lower as the twilight approached and their echo trace blended finally into the bottom echo".

LATERAL DISTRIBUTION OF FISH IN THE NET

PROCEDURE. Since the lateral distribution of the fish appeared to differ from one mesh to another and from set to set, the individual catches were analysed separately. The first step was to tabulate the numbers of fish of each species in successive segments of the net, each segment being approximately 1 foot (30 cm) wide and extending from the cork line to the lead line. Statistical tests were then applied to determine the probability that the fish were randomly distributed amongst the segments.

In one of the tests for randomness in the lateral distribution a contingency table was constructed showing the number of combinations of an empty segment next to an empty segment, an empty segment next to a segment containing 1 fish, an empty segment next to a segment containing 2 fish, etc. Expected frequencies of these combinations were then calculated from the row, column and grand totals in the table and the difference between the observed and expected frequencies subjected to a chi-square test (Snedecor, 1959; Steele and Torey, 1961). The adjustment for continuity was applied for 2×2 tables. The distribution was considered to be indistinguishable from random if the probability of obtaining a chi-square equal to or greater than that observed was 5% or more.

Another method of testing for randomness of lateral distribution was to calculate the coefficient of correlation, r, between the numbers of fish in adjacent segments of the net and then test the null hypothesis $r = 0$ by Student's t, where:

$$t = r \sqrt{(n-2) \div (1-r^2)}$$

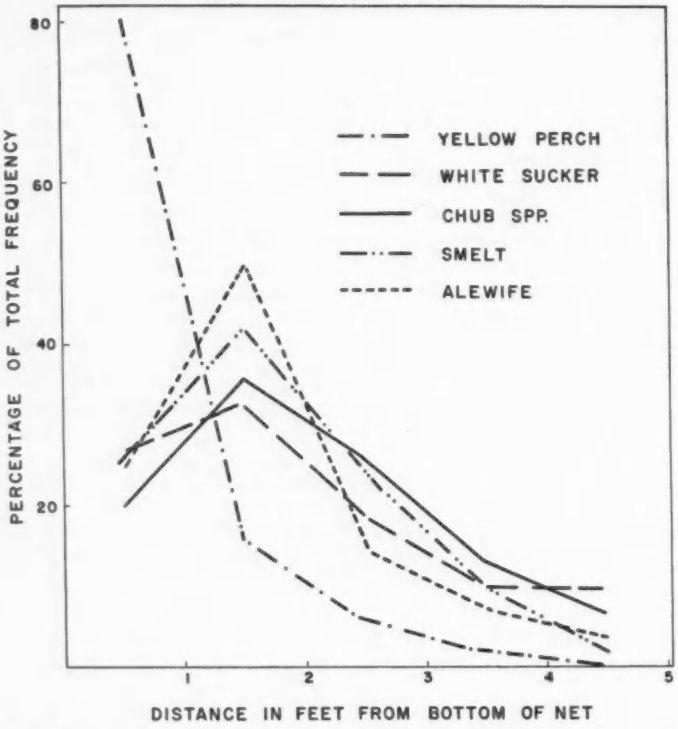

FIG. 1. Vertical distribution of yellow perch, white suckers, chub spp., smelt and alewives in experimental gill net gangs (pooled results of settings).

Here n is the total number of fish of a given species in the net. The null hypothesis was considered not to be disproven if the probability of obtaining a "t" value as large as or larger than that observed was 5% or more. Under such circumstances the lateral distribution of the fish was random or nearly so. A significant positive coefficient would on the contrary indicate bunching[4] while a significant negative coefficient would indicate dispersion[5].

The third means of analysing the lateral distribution was to test the significance of the difference between the observed and expected number of "runs" (Dixon and Massey, 1951; Siegel, 1956), where a run consisted of a succession of empty segments of net or a succession of segments containing 1 or more fish. The expected number of runs is calculated from the formula:

$$\mu = \frac{2\,n'n''}{n' + n''} + 1$$

[4]Bunched = less uniform than random.
[5]Dispersed = more uniform than random.

where n' represents the number of empty segments in the net and n'' the number of segments containing fish. The appropriate standard deviation is:

$$\sigma = \sqrt{\frac{2n'\,n''\,(2n'\,n'' - n' - n'')}{(n' + n'')^2\,(n' + n'' - 1)}}$$

The standard measure $(\mu - b)/\sigma$ can then be obtained and the corresponding probability found in a table of cumulative normal frequency distribution, provided that both n' and n'' are larger than 10. Here b represents the observed number of runs. Standard measures outside the range –1.96 to 1.96 occur with a probability of less than 5% and may be taken to indicate a significant departure from random distribution. Significant positive standard measures suggest bunching of the fish while negative values suggest that they are dispersed.

RESULTS. The results of the above tests are summarized in Table II[6] and in general they are consistent for a given catch. All three tests failed to indicate that the lateral distribution of the fish differed from random in the following instances: perch taken in 1.75- and 2-inch meshes on July 13–14 and August 4–5; smelt taken in 1-inch mesh on August 6–7 and August 7–8, and chubs taken in 1.75-inch mesh on August 6–7 and 7–8. On the other hand, the 3 tests suggest that the lateral distribution of the suckers caught in the 3.5-inch mesh on July 13–14 and of the smelt taken in the 1-inch mesh on August 4–5 was not random. The negative coefficient of correlation, and the greater-than-expected number of runs suggest that the suckers were dispersed. In contrast, a greater-than-expected number of 1×1 combinations in the contingency table, the positive coefficient of correlation, and a smaller than expected number of runs suggests that the smelt taken on August 4–5 were bunched along the net.

The alewives taken in the 1.5-inch mesh on July 13–14 and on August 4–5 also appear to have been bunched. This is shown by both the test for contingency and that for correlation but not by the test based on the number of runs. However, the test based on the number of runs can be disregarded for these 2 catches of alewives. It is the least sensitive of the 3 tests, since it takes no account of the numbers of fish in successive segments and depends only upon the presence or absence of fish. Moreover, this test probably does not apply at all to the July 13–14 catch of alewives, since there were fewer than 10 empty segments of net for that catch.

Finally, the test for contingency indicates that the perch taken in the 1.5-inch mesh on July 13–14 were bunched[7] but this conclusion is not supported by either the coefficient of correlation or the test based on runs. Nevertheless, the fact that there were 164 perch and 422 alewives concentrated in the bottom 3 feet (91 cm) of a 50-yard (46-m) section of net in this particular catch suggests

[6]The original data are too extensive to tabulate here. They are on file at the Ontario Department of Lands and Forests, Southern Research Station, Maple.

[7]The high value of chi-square for this catch indicates that the lateral distribution was not random while a greater than expected number of 1×1 combinations in the contingency table points to a bunched distribution.

TABLE II. Summary of the lateral distribution of fish in 50 yards (46 m) of gill net (150 yards for suckers).

Date	Mesh (inches)	Number of fish	Test 1			Test 2				Test 3	Conclusion: Randomness not disproved		
			R × C table			Correlation coefficient				Expected runs			
						r	Test for $r = 0$			$\mu - b$			
			d.f.	χ^2	P-interval		d.f.	t	P-interval	σ	1	2	3
Perch													
July 13–14	1.50	164	4	16.6	<0.01	0.143	133	1.66	0.10	–0.759	no	yes	yes
July 13–14	1.75	142	4	2.71	0.70 0.50	0.0854	150	1.05	0.30 0.20	0.647	yes	yes	yes
July 13–14	2	38	1	0.363	0.70 0.50	0.0814	158	1.03	0.40 0.30	0.836	yes	yes	yes
Aug. 4–5	1.75	43	1	0.041	0.90 0.80	0.0837	150	1.03	0.40 0.30	0.441	yes	yes	yes
Aug. 4–5	2	33	1	0.146	0.70 0.50	0.127	221	1.89	0.10 0.05	0.670	yes	yes	yes
Alewife													
July 13–14	1.50	442	4	10.6	0.05 0.02	0.325	133	3.84	<0.01	[a]	no	no	[a]
Aug. 4–5	1.50	28	1	8.68	<0.01	0.358	141	4.56	<0.01	1.05	no	no	yes
Smelt													
Aug. 4–5	1	27	1	4.33	0.05 0.02	0.396	149	5.15	<0.01	2.56[b]	no	no	no
Aug. 6–7	1	113	4	1.38	0.90 0.80	–0.0578	141	0.687	<0.50	0.493	yes	yes	yes
Aug. 7–8	1	114	4	6.36	0.20 0.10	0.0769	141	0.915	0.40 0.30	–1.34	yes	yes	yes
Chub													
Aug. 6–7	1.75	27	1	0.0665	0.80 0.70	–0.0221	157	0.278	<0.50	0.344	yes	yes	yes
Aug. 7–8	1.75	40	1	2.19	0.20 0.10	–0.119	157	1.49	0.20 0.10	–0.675	yes	yes	yes
Aug. 7–8	2	27	1	4.36	0.05 0.02	–0.137	165	1.77	0.10 0.05	–1.22	no	yes	yes
Suckers													
July 13–14	3.50	90	1	7.54	<0.01	–0.140	390	2.79	<0.01	–2.31[b]	no	no	no

[a]This test not applicable here (see text).
[b]Significant.

that the fish of both species were indeed extremely bunched. Hence the conclusion drawn from the test of contingency is probably correct. On the other hand the contingency test indicates that the chubs caught in 2-inch mesh on August 7–8 were not randomly distributed, whereas the test of correlation and expected number of runs suggests that the distribution was random. However there is no obvious explanation for this disagreement in the results of the tests of lateral distribution in this latter instance.

CONCLUSIONS AND SUMMARY

This paper describes a technique for studying the spatial distribution of fish captured in gill nets.

The vertical distribution of the fish was analysed graphically; the majority of the fish were taken in the lowest levels of the net. The maximum concentration of suckers, smelt, alewives and chubs occurred between 1 and 2 feet (30–61 cm) from the bottom of the net, whereas the maximum number of perch was found within 1 foot of the lead line.

In 9 of the 14 catches examined, the lateral distribution of the fish was close to random. In 4 of the catches the fish were contagiously distributed, and in 1 instance the lateral distribution was more uniform than random. There is no evidence in the present analyses that a particular type of distribution is associated with the size of mesh used. There is some suggestion of an association between the type of distribution and the species of fish. For example, bunching is demonstrated for alewives in 2 out of 2 instances; it is suggested for the perch in only 1 instance out of 5 and for the smelt in 1 case out of 3. It is not suggested at all in the 3 catches of chubs and the catch of suckers.

When there is a small catch in a large area of net, it seems reasonable to assume that the spatial distribution of the fish in the net corresponds to their distribution on approach. Under such circumstances bunching suggests that the fish approached the net in small schools whereas dispersion suggests they approached in a more uniform pattern.

However, as the number of fish caught increases, inferences about their distribution on approach to the net must be taken with increasing reservation. If the fish approach the net in successive "waves", then the first fish to be caught may frighten away later arrivals and cause the distribution to be dispersed. In other instances the first arrivals might serve as an attraction for those coming later and lead to bunching. These effects of avoidance or attraction are likely to be intensified as the duration of the set is extended. In future experiments the effect of this time factor might be tested by shortening the duration of the set or by setting two or more similar nets at once and lifting them after different periods.

The correspondence between the spatial distribution of fish in the net and that in the water may also be distorted to some extent by the escape of fish which are too big or too small to be entangled in the mesh in question.

ACKNOWLEDGMENTS

The authors are indebted to Dr F. E. J. Fry of the Department of Zoology, University of Toronto, for proposing the problem dealt with in this paper; to the late Mr J. C. Budd of the Research Branch, Ontario Department of Lands and Forests, for making available the facilities of the Fisheries Research Station at South Baymouth, and to the staff of that station for carrying out the netting, and helping to examine the catches. Special thanks are due also to Mr J. E. Paloheimo of the Fisheries Research Board of Canada for suggesting the statistical methods used in analysing the lateral distribution of the fish.

REFERENCES

DIXON, W. J., AND F. J. MASSEY, JR. 1951. Introduction to statistical analysis. McGraw-Hill Book Co., Inc., New York, 370 pp.

HASLER, A. D., AND J. R. VILLEMONTE. 1953. Observations on the daily movements of fishes. *Science*, **118**: 321–322.

MAEDA, HIROSHI. 1953. Ecological analyses of pelagic shoals. I. Analysis of salmon gill-net association in Aleutian waters. (2) Distribution of fishes on the gill net. *Bull. Japanese Soc. Sci. Fisheries*, **19**(4): 305–318.

MCCOMBIE, A. M., AND F. E. J. FRY. 1960. Selectivity of gill nets for lake whitefish, *Coregonus clupeaformis*. *Trans. Am. Fish. Soc.*, **89**: 176–184.

MOYLE, J. B. 1950. Gill nets for sampling fish populations in Minnesota waters. *Trans. Am. Fish. Soc.*, **79**: 195–204.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Inc. New York, 312 pp.

SNEDECOR, G. W. 1959. Statistical methods. Iowa State College Press, Ames, Iowa. 534 pp.

STEEL, G. D., AND J. H. TORIE. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill Book Co., Inc., New York, 481 pp.

The In-Vitro Maturation of the Parasitic Nematode, *Terranova decipiens*, from Cod Muscle[1]

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ABSTRACT

The larvae of the parasitic nematode, *Terranova decipiens*, from fish muscle will mature to the adult in in-vitro culture. This stage in the life cycle of this nematode normally occurs in the digestive tract of the seal. A rather complex medium was used. This medium was composed of a commercially available tissue culture preparation, Medium 199, to which had been added glucose, beef embryo extract, beef liver extract and antibiotics. The incubation time required for the appearance of the adult nematode in culture was approximately the same as in the seal digestive tract.

INTRODUCTION

The muscles of the Atlantic cod (*Gadus morhua*) and several other species of marine fish may become infested with the larvae of a parasitic nematode, *Terranova decipiens* (Templeman *et al.*, 1957; Scott and Black, 1960). The degree and the incidence of fish infestation is believed to depend on the location of the host's feeding area. The larvae, during this stage of the life cycle of the nematode, may often be seen coiled up within the muscle in what appears to be a cyst. Upon consumption of the infected fish by the seal, the larvae leaves the fish and matures to the adult male or female within the seal stomach (Scott, 1953), or intestine (Montreuil and Ronald, 1957). Fertilized eggs are passed in the faeces of the seal and subsequently hatch into ensheathed larvae (Scott, 1955). These larvae are then thought to be eaten by marine invertebrates and carried without development until the invertebrate is eaten by the fish. The larvae bore through the stomach wall of the fish entering the body cavity and muscles, completing the cycle (Templeman *et al.*, 1957; Scott and Black, 1960; Myers, 1960).

This nematode is not viable in all mammals (Grainger, 1959) nor does ingestion of large numbers of the larvae have any effect on the growth of dogs (Crampton *et al.*, 1960).

The control of a disease whose life cycle involves several hosts can be obtained either by interruption of this cycle through the removal of a host or by preventing infection or development. With this ultimate goal in mind the nutritional requirements for maturation of the nematode within the seal stomach was thought to be a logical area for further study. Many excellent morphological

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and ecological descriptions of *Terranova decipiens* have been published (Myers, 1960; Grainger, 1959). The changes in the anatomy that distinguishes the larvae from the adult can be identified easily.

Attempts have been made in the past to achieve the maturation of the larvae but were without success. Martin (1921), using a medium containing raw fish, the proteolytic enzyme pepsin, and hydrochloric acid to increase the acidity, found that he could only obtain development to the pre-adult stage. The pre-adult stage is a description given to a larva whose mouth parts have changed from the typical boring tooth to the three well-developed lips characteristic of the adult. There is no sign of gonadal development. Grainger (1959) accomplished this same pre-adult stage under much the same cultural conditions. The latter investigator found that pepsin was not required for pre-adult development but was involved in releasing the worm from the musculature of the fish. A temperature of 37° C and the presence of pieces of fish were thought to be essential for the molt to the pre-adult to take place. The adult stage could not be achieved.

The present investigation describes the conditions necessary for the development of the larvae nematode to the mature adult in in-vitro culture.

METHOD

Commercially freshly caught cod were filleted and the fillets containing nematodes were surface sterilized with a germicide[2] followed by immersion in 70% ethyl alcohol for several minutes. This treatment destroyed the worms on the surface of the fillet and reduced the possibility of microbial contamination, considered one of the important steps for successful maturation of the nematode. The use of a hypochlorite (chlorox) for surface sterilization (Weinstein and Jones, 1956) in a concentration of 250 ppm prevented maturation of the nematode beyond the pre-adult stage. Although the worms appeared healthy and had several molts they never were observed to develop gonadal tissue. The cysts were removed with a minimum amount of surrounding muscle, placed in sterile physiological saline solution, and incubated at 35° C for an hour or so to permit the worms to free themselves., The nematodes, randomly selected, were then washed in a physiological saline solution and five to ten larvae placed in 60 × 15 mm plastic tissue culture petri plates in two ml of medium. Cultures were prepared using a number of different commercially available animal tissue culture growth media[3].

The most desirable medium was selected on its ability to maintain vigorously active larvae. After considerable modification of this medium and the feeding rate, a medium composed of Medium 199 containing 10% beef embryo extract, 5% glucose and 10% fresh beef liver extract was chosen. Beef liver extract (supernatant) was made by centrifugation of an aqueous extract of ground fresh

[2]"Wescodyne", a general purpose detergent-germicide manufactured by West Chemical Products Ltd., Montreal, Quebec.

[3]Becton, Dickinson and Company Canada Limited, Toronto 10, Ontario.

liver (50:50 by weight) at 7500 × *g* for one hour. This extract could be stored frozen in dry ice. The pH of the medium was approximately 6.2. To keep the worms active the medium must be renewed at least once a day. The larvae will survive for long periods of time if the medium is not renewed, however, under such conditions the worms are not active and in general appeared to be in poor condition. Although asceptic conditions and techniques were employed, antibiotics were found necessary to reduce the hazard of microbial infection. The antibiotics streptomycin (50 units/ml), penicillin (50 units/ml), and mycostatin (25 units/ml) were added. The occasional resistant organism could be controlled with chloromycetin but prolonged use was avoided because of the observed deleterious effects on the nematode. The cultures were incubated at 35° C, a temperature considered optimal for the survival of *Terranova* in saline solution (Ronald, 1960).

The living nematodes were examined with the aid of a microscope throughout their culture. They were also examined after being preserved in 70% alcohol followed by clearing in lactophenol (Grainger, 1959).

RESULTS AND DISCUSSION

Three to six days after incubation in the culture medium, the larvae molted to the pre-adult stage. This stage in the maturation of the nematode could be determined by the loss of the boring tooth and the appearance of lips. The formation of the pre-adult occurred in all media incubated at 35° C. However, larvae kept in physiological saline solution at 35° C appeared to begin to molt and either died during or soon after molting. On the other hand, larvae placed in the above physiological solution at 5° C did not change morphologically, remaining as active larvae for several weeks. The pre-adult molt was thought to be initiated by the increased environmental temperature from the normal low temperatures of the sea to that of the stomach of the seal. The culture medium, adjusted to pH 2.5 with hydrochloric acid just prior to use in order to simulate stomach conditions and renewed daily, did not permit the development of the worms beyond the pre-adult stage.

The formation of a cap-like structure over the head of the larvae which was fastened securely to the bottom of the culture dish was observed occasionally before the appearance of the pre-adult stage. When the larvae were shaken loose a thimble-shaped cap remained fastened to the plastic surface. On closer examination a hole was observed in the end of the cap corresponding to the mouth area. Presumably this structure might enable the larvae to remain fastened to the stomach or intestinal wall during the molt.

Larvae freshly removed from fish muscle and transferred into culture medium maintained vigourous activity for a day or so and then became relatively quiet for several days. During this quiet period molting took place. The intestine of the newly transferred larvae was creamy white, smooth, and opaque. As a result, observation of the gut content could not be made. On the other hand, the variation in the density of gut content of the pre-adult and the adult could be

observed with transmitted light. The intestinal tract of the pre-adult and the adult, when not feeding, is collapsed accordian-like and the worm likewise is reduced in length. The nematode is generally in this condition after being in the culture medium for twenty-four hours. Within the first hour of the renewal of the medium, the worm is refilled with medium and again extended and active. It was common to observe up to one-half of the intestinal volume to be renewed at once. The muscle in the oesophagus could be seen pumping in the medium at such a rate as to create a vortex in the medium at the mouth. Occasionally, air would be taken down to form a bubble in the intestinal tract. The passage of this air through the intestine could be observed with the naked eye. The movements of the sphincter muscle which controls the intestino-rectal valve appeared independent of the muscle feeding movement in the oesophagus. Thus a large volume of medium could be consumed without passage of fluid from the anus. After feeding, the worm was greater in length and width than before feeding and was quite turgid. If the culture medium was supplied continuously the gut was always observed to be full and the worm turgid and very active.

Macroscopic morphological change in the size of the worm following the formation of the pre-adult was very slow and was not observed until after approximately two to three weeks incubation. Sexual development was not observed externally during this period. The dimensions of the live worm were difficult to note due to the change in size with feeding. Noticeable, however, was the sudden change to the mature adult which occurred within two to three days following the quiet period noted above. The pre-adult female suddenly increased in length and width and developed gonadal tissue (Fig. 1). The adult male was recognized at approximately the same time as the female. The male did not show the increase in size typical of the female but did develop recurved, dorso-ventrally flattened tail characteristic of the male. All females were not of the same dimensions when gonadal tissue was observed and did not develop to the same adult size regardless of the time of incubation. This appearance of gonadal tissue independent of the size of the worm also appeared to be true for the male. Both male and female developed in the same culture. The time required for the larvae to develop to the adult in in-vitro culture was analogus to the maturation time of sixteen to twenty days required for the female worm observed in the seal digestive track (Scott, 1953). An average of four out of five worms survived to the adult stage. Death of the worm before the adult stage was in many cases believed to be due to infection or accidental injury. Bacterial infection which could not be controlled with antibiotics eventually would destroy the nematodes.

Eggs could be observed in the sexually mature female ovaries (Fig. 2–6). The first appearance of eggs in the uterus occurred from one to three weeks after the appearance of the vulva. Interesting is the observation that the medium most suitable for the development of this nematode parasite of fish muscle contained liver extract. Whether the requirement for liver extract was obligatory or not was not determined. However, the nematode parasites of coeleopterous larvae in soil, *Neoaplectana glaseri* (Stoll, 1953); of rodents, *Nippostron-*

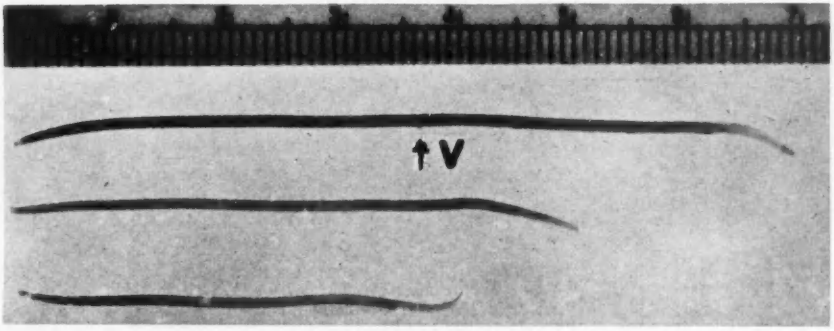

FIG. 1. Photograph showing the size difference between an average larva (bottom) and female adults (top two worms) (V = Vulva).

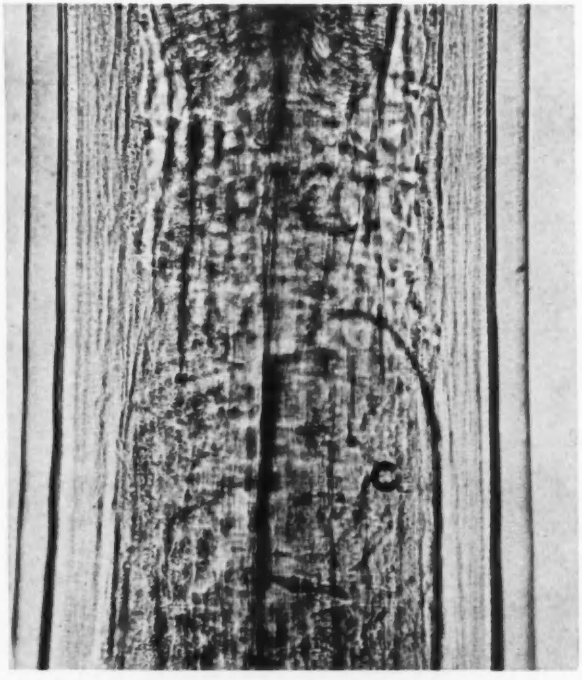

FIG. 2. View of oesophageal region of adult showing intestinal caecum (C).

FIG. 3. View of head region of adult showing lips.

FIG. 4. View of tail region of female adult.

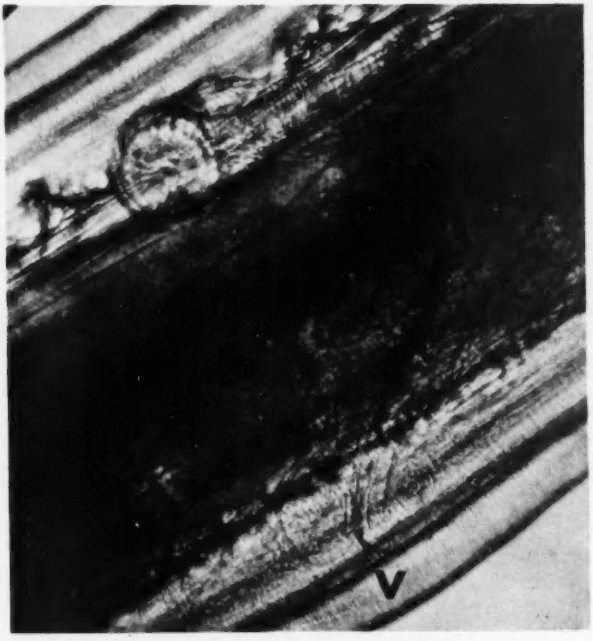

FIG. 5. View of vulva region of sexually mature nematode. (V = Vulva).

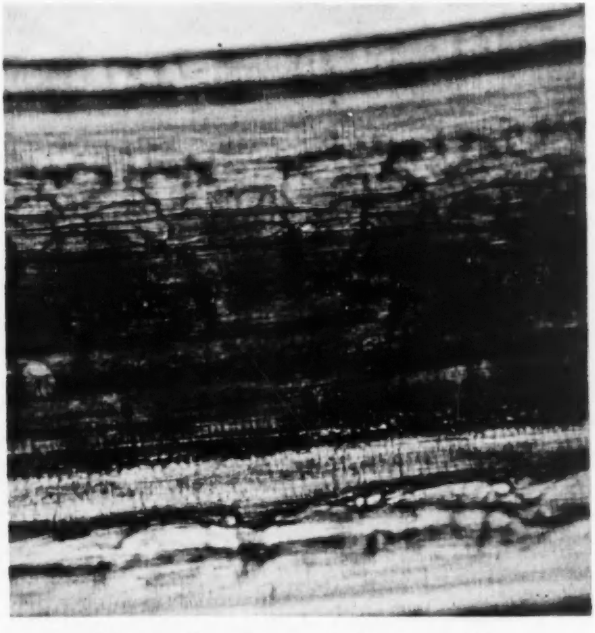

FIG. 6. View of uterus area showing eggs (e).

gylus muris (Weinstein and Jones, 1956) and the free living nematode *Caenorhabditis briggsae* (Tomlinson and Rothstein, 1962), all of which have been cultured in-vitro have a requirement for or are benefitted by the presence of liver extract in the culture medium.

REFERENCES

CRAMPTON, E. W., E. DONEFER AND D. J. SCHAD. 1960. Effect of the ingestion of *Porrocaecum* (codworm) on growth, voluntary intake and feed efficiency of beagle pups. *J. Fish. Res. Bd. Canada*, **17**: 501–505.

GRAINGER, J. N. R. 1959. The identity of the larval nematodes found in the body muscles of the cod (*Gadus callarias* L.). *J. Parasitology*, **49**: 121–133.

MARTIN, O. 1921. Uber ascaridenlarven aus dem fleische von seefischen. *Z. Infekt. Kr. Haustiere*, **22**: 13–36.

MONTREUIL, P. L. J., AND K. RONALD. 1957. A Preliminary note on the nematode parasites of seals in the Gulf of St. Lawrence. *Canadian J. Zool.*, **35**: p. 459.

MYERS, B. J. 1960. On the morphology and life history of *Phocanema decipiens* (Krabbe, 1878) Myers, 1959. *Canadian J. Zool.*, **38**: 331–344.

RONALD, K. 1960. The effects of physical stimuli in the larval stage of *Terranova decipiens*. I. Temperature. *Canadian J. Zool.*, **38**: 623–642.

SCOTT, D. M. 1953. Experiments with the harbour seal, *Phoca vitulina*, a definitive host of a marine nematode, *Porrocaecum decipiens*. *J. Fish. Res. Bd. Canada*, **10**(8): 539–547.

1955. On the early development of *Porrocaecum decipiens*. *J. Parasitology*, **41**(3): 321–322.

SCOTT, D. M., AND W. F. BLACK. 1960. Studies on the life-history of the ascarid *Porrocaecum decipiens* in Bras d'Or Lakes, Nova Scotia, Canada. *J. Fish. Res. Bd. Canada*, **17**(6): 763–774.

STOLL, N. R. 1953. Axenic cultivation of the parasitic nematode, *Neoaplectana glaseri*, in a fluid medium containing raw liver extract. *J. Parasitology*, **39**: 422–444.

TEMPLEMAN, W., H. J. SQUIRES AND A. M. FLEMING. 1957. Nematodes in the fillets of cod and other fishes in Newfoundland and neighbouring areas. *J. Fish. Res. Bd. Canada*, **14**(6): 831–897.

TOMLINSON, G. A., AND M. ROTHSTEIN. 1962. Nematode biochemistry. I. Culture methods. *Biochim. Biophys. Acta. Previews*, **2**(2).

WEINSTEIN, P. P., AND M. F. JONES. 1956. The *in-vitro* cultivation of *Nippostrongylus muris* to the adult stage. *J. Parasitology*, **42**: 215–236.

Sympatric Occurrence of Two Species of Humpback Whitefish in Squanga Lake, Yukon Territory[1]

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ABSTRACT

Squanga Lake in the Canadian headwaters of the Yukon River contains two species of humpback whitefish, characterized by modal first arch gill raker counts of 23 and 28 but with overlap in the range of counts. The species can be separated more sharply by raker counts of the second arch, also with modes of 23 and 28. Seven other morphometric characters not correlated with gill raker count each have significantly different means, but some overlap, between the species.

In June the species with high raker count mainly occupies the pelagic zone, while the low count species occupies the bottom layers at all depths. The high count species feeds mainly on plankton, the low count species on bottom organisms. The high count species spawns in inlet and outlet streams in November and December. Gonad development in June suggests that the low count form spawns later, in localities unknown. Samples from early winter spawning runs contained exclusively high count individuals. A few fish, probably hybrids, had raker count corresponding to one species and most other morphological characters corresponding to the other. Tentative names for the species are *Coregonus clupeaformis* (high gill raker count) and *Coregonus pidschian*.

INTRODUCTION

This study deals with two species of humpback whitefish[2], genus *Coregonus*, which are almost identical in superficial appearance but which co-exist in a lake in the Yukon River headwaters without appreciable interbreeding. Known cases of sympatric occurrence of more than one species of humpback whitefish are rare in North America. They are important in sorting out taxonomic relationships between similar but not identical forms which have been named from different places. They also raise interesting questions about ecological separation between similar species, and about possible mechanisms preventing their mass hybridization.

HISTORY OF SQUANGA LAKE INVESTIGATIONS

In 1934 six specimens of whitefish were taken by Mr Alfred Dickson from Squanga Lake, Yukon Territory, Canada, in November or December, and were sent to Professor J. R. Dymond at the Royal Ontario Museum. The catalogue entry for these specimens (ROMZ 8729 to 8734) reads: "Caught in 18 inches water during spawning run. Mr. Dickson says this variety of whitefish is found

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[2]"Humpback" whitefish is used to indicate species of *Coregonus* excluding species of "ciscoes" and excluding the broad whitefish *C. nasus* (Lindsey, 1962).

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only in Squanga Lake and upper tributaries, 2,800 feet above sea level. In his first letter he said they did not exceed six inches in length". Counts and measurements from these specimens were later published (Dymond, 1943). Their gill raker counts (given as 26 to 30, average 28) were the highest of any northwestern *Coregonus* studied by Dymond, but he identified them as members of the wide-ranging and variable *C. clupeaformis*.

In 1945 Dr V. C. Wynne-Edwards undertook a survey of fishery resources in Yukon Territory for the Fisheries Research Board of Canada. He probably visited Squanga Lake and examined whitefish there, although no specimens seem to have been preserved. He later wrote (Wynne-Edwards, 1952; p. 13): "there are some additional types [of *Coregonus*] peculiar to special districts, for example the "squanga" found in Squanga Lake, Southern Yukon Territory, which is notable for its extraordinary development of rough warts, the so-called nuptial tubercles, from head to tail; for the fact that there are 26 rows of scales, counted diagonally down the side of the body, which is more than in any other described form; and for having 28 to 29 gill-rakers, the highest number of any nearctic *Coregonus*. Superficially, and in some fundamental characteristics, it comes closest to *C. muksun aspius* from Lake Onega in Russia. At Squanga Lake the common whitefish (*nelsoni*) is also present, but the two are said to have different spawning beds."

In 1955 Walters pointed out that *C. muksun aspius* had from 44 to 72 gill rakers, and therefore did not correspond to the Squanga Lake fish. He wrote: "According to Wynne-Edwards (1952) two kinds of hump-backs are found in Squanga Lake . . . The *squanga* is *C. clupeaformis* (which see), but Wynne-Edwards did not give gill raker counts for the other kind, and it is uncertain what this other fish may be".

On May 20, 1958, accompanied by Messrs J. D. McPhail and D. Miller, the writer set gillnets in Squanga Lake and obtained 40 specimens. These subsequently revealed a bimodal distribution of gill raker count, with a major mode at 24 and suggestion of a second at 29.

In June 1960 a more intensive study was launched. For two weeks Messrs A. W. Beadell and E. D. Lane, graduate students at the University of British Columbia, collected some 1200 specimens with gill nets and seines, and obtained information on depth distribution and feeding. During the first few days they were assisted by Mr McPhail and myself, and by Game Warden Barry Paull and Dr T. G. Northcote who sounded the lake and made limnological observations. A small collection was also taken by gill net on August 4, 1960. Finally, samples of spawning whitefish from inlet and outlet of the lake were obtained on November 5, 24 and 28, 1960 by Fisheries Officer W. K. Elliot and shipped, frozen, to the University of British Columbia.

DESCRIPTION OF SQUANGA LAKE AND SURROUNDINGS

Squanga Lake lies in southern Yukon Territory 32 miles (51 km) north of the British Columbia border, on the Alaska Highway 11 miles (18 km) west of the outlet of Teslin Lake. The surroundings are broken uplands with some

mountains rising to 6000 feet (1830 m), forming part of the Yukon Plateau in which rise the headwaters of the Yukon River. Summers are short and cool; winters are long and cold; annual precipitation is light (about 14 inches (36 cm) at Teslin) and spread fairly evenly through the year.

Squanga Lake, at an altitude of 2593 feet (790 m), lies 354 feet (108 m) higher than Teslin Lake. Its outlet drains by a short stream into Squanga Creek, which enters the Teslin River 8 miles (13 km) below Teslin Lake (Fig. 1). Ascent of fish from Teslin River is blocked by falls with a drop of at least 180 feet (55 m) in the lower quarter mile of Squanga Creek.

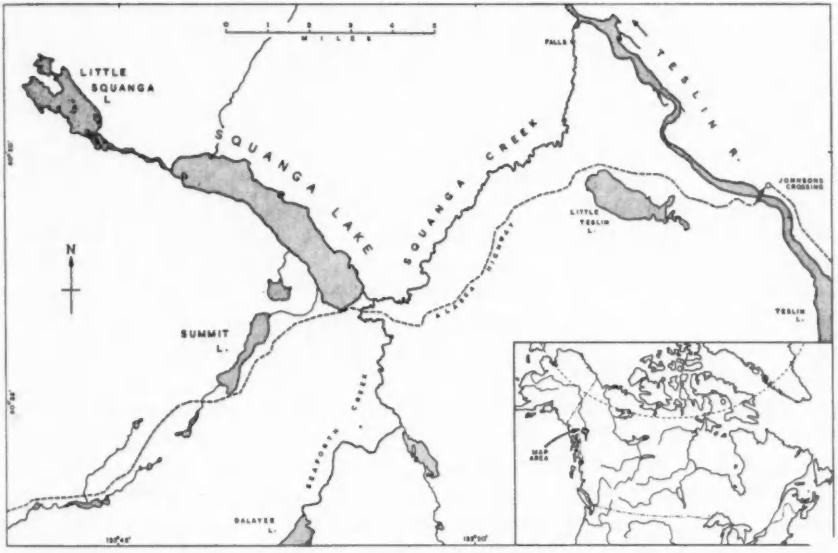

FIG. 1. Map of Squanga Lake drainage.

Squanga Lake has a length of 5½ miles (8.8 km) and an average width of ¾ mile (1.2 km). There are extensive shallows, with 21% of the lake area less than 10 feet (3 m) deep; a deep central trench 2 miles (3.2 km) long and roughly 600 feet (183 m) wide contains water over 100 feet (30 m) deep. Maximum depth is unknown but is at least 130 feet (40 m).

Little Squanga Lake to the northwest (Fig. 1) is tributary to Squanga Lake by a shallow stream with only a few feet drop; probably no serious block to the passage of fish is present in this stream, from which spawning whitefish have been taken in early winter. A few soundings in Little Squanga Lake yielded a maximum reading of 50 feet (15 m).

Another smaller tributary lake, Summit Lake (Fig. 1) lies about 150 feet (46 m) higher than Squanga Lake; the small stream connecting these two lakes probably does not provide passage for whitefish.

No other lakes are directly tributary to Squanga Lake, but Seaforth Creek (Johns River) which joins Squanga Creek just below the outlet of Squanga Lake (Fig. 1) drains several other lakes to the south. The largest, Dalayee (locally known as Trout) Lake, is 6 miles (9.6 km) long and lies at 3184 feet (972 m); others are Teenah Lake 2½ miles (4 km) long with an altitude of roughly 2850 feet (870 m), and Seaforth (or Fish) Lake, 1¼ miles (2-1 km) long and between 2600 and 2700 feet (793 and 823 m) in altitude. The Seaforth Creek drainage, 25 miles (40 km) in length, is rather inaccessible, and was not explored during this study, but some information on its fishes was obtained from trappers who visit the area in winter.

Squanga Lake has relatively high total dissolved solids (243 parts per million), extensive *Chara* beds, abundant bottom organisms in the shallows (over 25 per 6-inch (15-cm) Ekman dredge sample), and, during June 1960, moderately abundant plankton (total 90 foot (27 m) vertical haul with No. 10 Wisconsin plankton net yielding 2.3 ml settled volume of plankton; Secchi disc reading 13 feet (4.0 m)). Whitefish were so numerous that in the shallows large schools were often observed fleeing before an advancing boat, and on still evenings or nights the lake surface was sometimes densely marked by the rises of whitefish. These combined observations place Squanga Lake high in the scale of productivity when compared with British Columbia lakes (Northcote and Larkin, 1956). Limestone exposures in the area, including one half a mile south of Summit Lake, probably contribute to the high productivity. In 1960, ice left the lake on about 20 May; by 8 June thermal stratification was developing with a thermocline extending down to 40 feet (12 m). (Fig. 3).

In addition to *Coregonus*, Squanga Lake contains burbot (*Lota lota*), and northern pike (*Esox lucius*). Neither of these predators seem very abundant, but some large individuals of each species were captured. Arctic grayling (*Thymallus arcticus*) were largely confined to the streams. The slimy sculpin (*Cottus cognatus*) was the only other species taken.

This is a surprisingly small list of species. Both the lake trout (*Salvelinus namaycush*) and the round whitefish (*Prosopium cylindraceum*) are abundant in many comparable lakes in the region, and might be expected to thrive in such a productive lake. Moreover, lake trout are reported to occur in Dalayee Lake in the same drainage system. Conceivably the unusual abundance of humpback whitefish in Squanga Lake produces such heavy predation on eggs that lake trout are unable to reproduce there.

Specimens of *Coregonus* were also taken in Little Squanga Lake and in Summit Lake. A population of very small whitefish was reported to inhabit a small lake between Seaforth and Teenah Lake.

Teslin Lake to the east contains at least 14 species of fish, but their access to Squanga Lake is now cut off by falls. The Squanga Lake fish fauna may, however, have entered from the west via the Lewes River–Atlin Lake branch of the Yukon River, rather than from the east via Teslin River. Tributaries to Summit Lake are separated by only ⅔ mile (1.1 km), and a few feet of elevation, from headwaters of Little Atlin Creek which flows westward. Remnants of

glacial meltwater channels which at one time drained south-westward now occupy this valley along which the Alaska Highway runs. The whole region abounds in glacial drift, elevated terraces and old water courses. The margin of the great unglaciated area of the Yukon basin lies about 150 miles (241 km) to the northwest. Present fish distributions in the Southern Yukon Plateau probably reflect the complex history of alterations in drainage patterns during the recent glacial retreat.

METHODS

All gill nets used were of monofilament nylon (filament diameter 0.20 mm) which was almost invisible under water and caught fish effectively during daylight. Three nets, each 25 feet (7.6 m) deep and 50 feet (15.2 m) long, were of 1½, 2 and 2½ inches (3.8, 5.1 and 6.3 cm) stretched mesh respectively. Ten others were each 8 feet (2.4 m) deep and 40 feet (12.2 m) long, of mesh sizes from 1½ to 3½ inches (3.8 to 8.9 cm) stretched mesh. Nets were set at various locations and depths, sometimes on the bottom and sometimes suspended along the surface by auxilliary floats; all sets were held in position between vertical lines running from floats to anchors at either end of the net gang. Between 7 and 18 June 1960 a total of 9 surface nettings and 19 bottom nettings were conducted, covering most areas of the Squanga Lake and its outlet, in water depths from 4 to 130 feet (1.2 to 40 m). One gang of nets also was set in Little Squanga Lake and one in Summit Lake.

Fish were also sampled by periodic sweeps of a 60 foot (18 m) beach seine, 8 feet (2.4 m) deep, equipped with a central pocket. All seinings were at a sand beach at the south end of the lake; the seine was in each case set parallel to shore and 100 feet (30 m) out from it, in 4 feet (1.2 m) of water; each end was then drawn straight in towards a marker on shore.

All whitefish taken were examined while fresh by the field party. Gill rakers were counted on the left arch by cutting from the lower corner of the opercular slit forward to the symphysis, and folding the gill cover upwards; rakers were then counted using a low power magnifying glass and artificial illumination. Counts so made are referred to as "field counts". Many of these fish were individually tagged and preserved in formaldehyde, and later examined in the laboratory, where gill raker counts were made on arches which had been cut free and examined under a binocular microscope. Every bony rudiment was included in the gill raker counts. Gonad volumes and volumes of stomach contents were also measured by the field party, using displacement of water level in graduated tubes. Identification of stomach contents in the field was limited to rough categorization, using a magnifying lens. Fish length measurements refer to fork length obtained with a measuring board.

Morphometric studies are based on specimens preserved in formaldehyde and later transferred to 40% isopropyl alcohol. A measuring board was used equipped with travelling pointer mounted at right angles to the long axis of the specimen and registering to 0.1 mm on a dial. The following measurements were recorded as projected distance backward from the snout of the fish: "pre-postorbital" (to the posterior rim of the bony orbital margin), "head length"

(to the posterior margin of the bony opercle, excluding the skin flap behind), "pectoral origin" (to the junction of the anterior face of the pectoral fin with the fin bent outwards perpendicular to the long axis of the body), "pectoral length" (calculated by subtracting the preceding measurement from the distance from snout to posterior tip of the longest pectoral ray with the fin lying backwards along the body), "pelvic origin" (to the anterior face of the pelvic fin when bent outwards perpendicular to the body), "fork length" (to the posterior tip of the central caudal fin ray).

The following measurements were taken with dial calipers reading to 0.1 mm: "head depth" (from the occiput to the breast, perpendicular to the long axis of the body), "body depth" (from the origin of the dorsal fin to the ventral surface of the body perpendicular to its long axis).

GILL RAKER COUNT AND DEPTH DISTRIBUTION

Frequency distribution diagrams of gill raker counts (Fig. 2) show that most fish taken in bottom gill net sets in Squanga Lake had 25 or fewer gill rakers, with modal value at 23. In sharp contrast, fish taken in surface nets floating over deeper water were distinctly bimodal in gill raker counts with a second peak at 28 rakers. While *some* of both high and low count fish were taken in each type of net set, high counts were rare in bottom sets but were as common as low counts in floating sets.

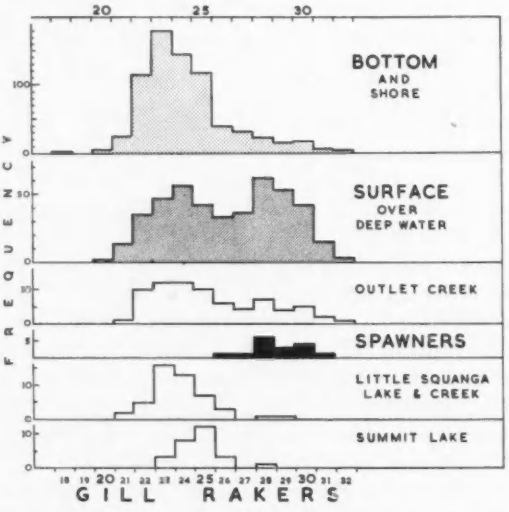

FIG. 2. Field gill raker counts (left side, first arch) of whitefish captured at different depths and localities. All taken by gill net in June, 1960, except "spawners" taken in inlet or outlet streams in November or December (1934 and 1960 combined).

Not only were high counts more frequent in floating sets, but amongst these the highest proportion of high counts occurred in the sets over deepest water (Fig. 3). The surface nets (either 8 or 25 feet (2.4 or 7.6 m) deep) floating in 40 feet (12 m) of water caught only 36% high count forms (defined as having 27 or more gill rakers), while similar nets floating over 80 feet (24 m) of water caught 69% high count forms.

Similarly, amongst bottom sets (nets 8 feet (2.4 m) deep), high count forms were completely absent in the deepest set (in from 40 to 130 feet (12 to 40 m) of water, average 85 feet (26 m)) but in shallower water they comprised from 0% to 16% of the catch. Nets set in the outlet of Squanga Lake contained 31% high count forms (Fig. 2 and 3).

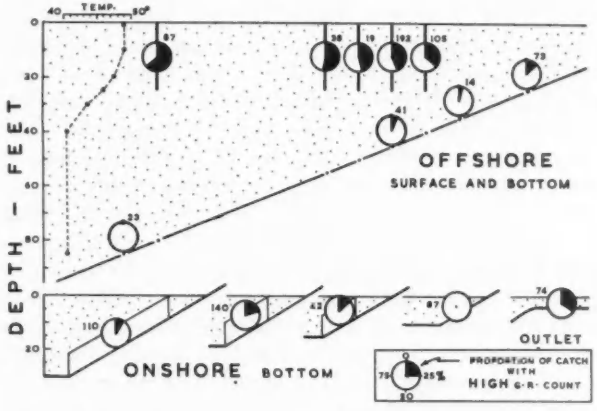

FIG. 3. Proportions of whitefish with high gill raker count (27 or more), indicated by black segments of circles, in gill net catches from different depths in Squanga Lake, June, 1960. Each circle represents from 1 to 3 nettings. Numbers indicate sample sizes.

Some diurnal change in depth distribution of the two forms is suggested by one set of nettings. A floating gang of nets set over 45 feet (14 m) of water was left in over a 36 hour period and the fish were removed four times. During the experiment moderate to strong winds prevailed, and the nets became encrusted with plankton. Proportion of whitefish with high gill raker counts ranged from 17% in the morning period (0900 to 1515 hours), to 74% in the afternoon (1515 to 1930 hours), with successive overnight catches having 34 and 29%. A gang of nets set on the bottom in the same place during the morning period took only 5% of the high raker form.

On another day a floating set over 40 feet (12 m) of water caught no fish with high raker counts amongst 10 taken between 1330 and 1930 hours. The net was left in place, and during the calm evening fish were seen rising over the entire visible surface of the lake. Next morning (0945) the surface net contained 30 fish, 10 of which had high raker counts.

These changes in distribution of gill raker count at different times in one location appear significant. Therefore, spatial separation between low and high count forms may be greater than indicated by most net catches, which cover several hours and lump together fishes which arrived at the net at different times. Net sets, unless emptied at short intervals, may obscure the fact that whitefish may travel in homogeneous schools whose composition may be stable for long periods.

Most floating gillnets were 25 feet (7.6 m) deep; while their upper portions fished the pelagic zone, their lower portions, particularly in the shallower sets, may have taken fish associated with the bottom zone. Position of fish in the nets was not recorded in detail, but it was noted that, during the 36-hour set just described, fish were confined to the lower two-thirds of the net during that period when the lowest proportion of high raker count forms was taken. Stomach contents of captured fish, discussed in the next section, also suggest that some fish taken in floating nets had recently been on the bottom.

Marked onshore movement of adult whitefish during low light intensities was demonstrated by hourly beach seine hauls made repeatedly at the same site on June 7–9. During daylight a maximum of 10 fish, and usually none, were taken in the seine, and no fish were seen close to shore. Between 2100 and 0100 hours the hourly catches were high, with a maximum of 135 in the seining at 2300 hours. Catches fell to nearly zero at dawn, and remained there until the following dusk, when they again rose sharply. Samples of the night time catches contained about 20% of the form with high gill raker counts.

Temperature may be a factor in producing the separation shown in June 1960. Slight temperature stratification was beginning to develop (Fig. 3), and the high count form was largely confined to the warmer layers of the open water. Some (although a smaller proportion of the total catch) were found in the nets set out from shore, and many were taken close to or in the warm outlet stream. This distribution may only indirectly reflect temperature, in that the next section will suggest that the high count form feeds primarily on plankton, which was probably most abundant in the surface layers.

GILL RAKER COUNT AND FOOD

Stomachs of some netted fish were examined in the field. Food organisms were not identified in detail and sampling of stomachs was uneven; nevertheless enough information is available to show a striking divergence in food of whitefish having low and high gill raker counts.

In Table I, each fish has been classed as containing either benthic organisms or pelagic and surface organisms, or some of both the foregoing categories, or no food at all. Benthic items included clams, snails, *Chara* and chironomid larvae. (The last-named are not necessarily confined to the benthic zone (Mundie, 1959); inclusion of chironomid larvae as "plankton" would not however alter the marked difference in feeding habits shown in Table I.) Pelagic and surface items included primarily small crustacean plankton, with some terrestrial insects. Other items found in some stomachs included dipteran pupae, fish

TABLE I. Comparison of identifiable food items in stomachs of Squanga Lake whitefish with low (26 or fewer) or high (27 or more) gill raker counts. Number of stomachs in parenthesis.

Place of capture	Stomachs with Benthic food	Pelagic and surface food	Both	Empty
	%	%	%	%
Low gill raker count				
Floating sets (12)	42	42	16	0
Bottom sets[a] (48)	83	4	13	0
Beach seines (19)	95	0	5	0
Total: (79)	80	9	11	0
High gill raker count				
Floating sets (35)	6	80	8	6
Bottom sets[a] (24)	4	46	13	37
Beach seines (7)	14	57	0	29
Total: (66)	6	65	9	20

[a] Bottom sets include samples from outlet.

scales, wood and unidentifiable detritus; stomachs containing only these items were excluded from Table I. Samples from collections taken at 14 different localities have been combined in Table I. All but one sample included both low and high count forms, although not in the same proportions.

Of fish with low gill raker count, 80% contained exclusively benthic food. Within the *low* count form, very few taken in beach seining or nets set on the bottom had eaten exclusively pelagic food, but 42% of those taken in nets floating over deep water contained exclusively pelagic (primarily crustacean plankton) organisms. Conversely, amongst fish with *high* gill raker count the proportion with exclusively pelagic or, less often, surface organisms was highest in the floating nets and lower in bottom sets or beach seined samples. Also, in the latter habitats many high count fish had wholly empty stomachs; more had, in fact, taken no food than had turned to a diet of bottom organisms. This contrasts with the low-rakered form, none of which had empty stomachs, even when taken in the pelagic habitat.

GILL RAKER COUNT OF EARLY WINTER STREAM SPAWNERS

Samples of spawning whitefish were obtained from Squanga Creek below Squanga Lake (November 5 and 24, 1960), from the creek below Little Squanga Lake (November 28, 1960), and from the "spawning run" (November–December 1934, ROM specimens). All 1960 samples were taken from under ice cover. Both ripe males and females were included and many specimens were strongly tuberculate. Gill raker counts of the 16 specimens examined are shown combined in Fig. 2 as "spawners". None of these fish had fewer than 26 rakers. The likelihood of drawing such a sample at random from the combined "population"

of counts from the whole lake is wholly remote. Unfortunately no concentration of spawners of the low raker type has been discovered. Nevertheless, gill raker counts of these early winter stream spawners offer strong evidence of at least partial segregation of the two forms of whitefish during reproduction.

SPAWNING TIME

Although spawning time and place of the form with low raker counts have not been discovered, indirect evidence is available from the size of gonads in fish taken in June, 1960. Displacement volume of gonads have been plotted on logarithmic scale against fork length in Fig. 4. In both males and females,

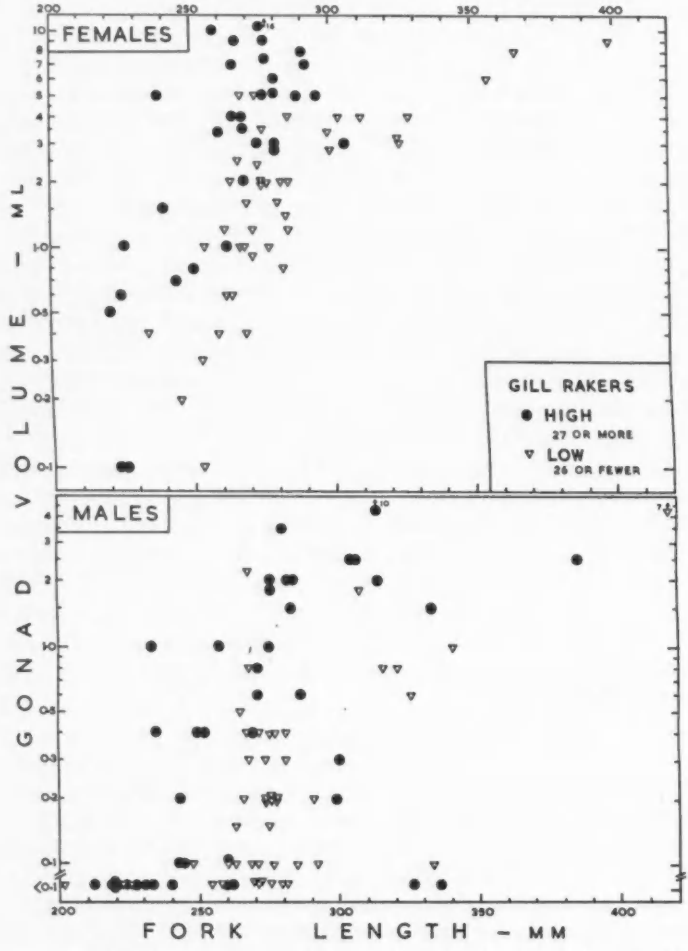

FIG. 4. Gonad volumes (logarithmic scale) and fork lengths of Squanga Lake whitefish taken in June, 1960.

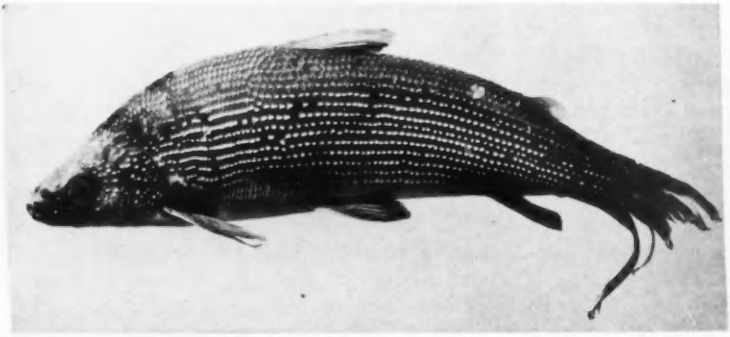

FIG. 5. Preserved male whitefish taken in Squanga Lake outlet 5 Nov. 1960, showing spawning tubercles.

the gonads in June were proportionately better developed in fish with high raker counts than in those with low. Presumably most of the high count forms had spawned about six months previously (in November and December 1959) and the gonads were partially developing preparatory to the next spawning. The small size of gonads in low count fish suggests that they had spawned more recently, perhaps in late winter, and by June had recovered only little.

The strong development of tubercles on spawning high count fish, mentioned by Wynne-Edwards (1952), is illustrated in Fig. 5. Tubercles were most pronounced in males but were present in both sexes taken in the spawning streams in November. No tubercles were visible on any fish taken in June, 1960, in the Squanga Lake area, with the exception on two females with low gill raker count captured in Little Squanga Lake. These both contained well-developed eggs, and bore tubercles similar to but not so pronounced as those on high-rakered November spawners. Nine of the males with low counts taken in Summit Lake had well-developed testes, but they bore no tubercles. In both Little Squanga and Summit Lakes spawning of the low-rakered form may be somewhat later than in Squanga Lake, and the few specimens still ripe in June may have been the remnant of late winter or early spring spawning. In any event, tubercles on two low-count females suggests that this nuptial development may not serve to separate the two forms. Koelz (1929) stated that both males and females of all species of *Coregonus* in the Great Lakes have tubercles at spawning time.

GILL RAKER COUNT AND OTHER MORPHOLOGICAL CHARACTERS

The five gill arches, which in laboratory examination were removed as a unit, were cut along the mid-dorsal line and spread out for examination under a dissecting microscope. Gill rakers were counted on left and right sides of both the first and second arches.

Comparison between field and laboratory counts on tagged specimens showed that about half the field counts on the first left arch were correct, while most of the remainder were one raker too high or too low. One of the two workers involved tended towards high counts, the other towards low. The net effect of errors in field counts was probably to increase the apparent dispersion of gill raker counts slightly but not to introduce an important bias in means.

Comparison of gill raker numbers on the first and second arch showed that amongst fish with high overall counts the second arch usually had equal, or, frequently, one more raker than the first, while in fish with low counts, the second arch usually had one or two fewer rakers than the first. Hence, sharper bimodality occurred amongst counts on the second arch than on the first in Squanga Lake fish (Fig. 7). The second arch has therefore been used in categorizing individuals as either "low count" (25 or fewer rakers) or "high count" forms (26 or more), for comparison of other morphological features.

Asymmetry of gill raker count between right and left arches occurred significantly more often in low than in high count forms. Only 10% of low count forms had no bilateral asymmetry in either first and second arches. No tendency towards right or left-handedness was noted. Where the two sides differed, the lowest count was used in categorizing a fish.

For morphological study, tagged specimens were selected such that their previously recorded field gill raker counts (first arch, left side) corresponded approximately in frequency distribution to the distribution of all fish caught in floating net sets (Fig. 2). Most specimens chosen had been taken from floating sets. Some fish from Little Squanga Lake, and some from the spawning run, were also included for detailed study. The 72 fish so chosen are intended to be roughly representative of a random sample from the pelagic area, in so far as counts on the first gill arch are concerned.

No morphological character other than gill raker count was found with sharply bimodal distribution, but many differed significantly when means for low count and high count forms were compared. The seven most satisfactory characters are listed in Table II. Many others also differed noticeably in mean between the two forms, but are not included for reasons stated below.

TABLE II. Body proportions, as percent fork length, of 72 Squanga Lake whitefish, showing their usefulness in separating fish of low and high gill raker count.

Character	GR II Low, < 26 Mean (Range)	GR II High, > 25 Mean (Range)	Utility in separation
			%
Pectoral origin	18.6 (16.2 –21.0)	16.9 (14.7 –19.5)	81
Body depth[a,b]	20.6 (17.9 –23.2)	22.5 (18.7 –24.5)	80
Pectoral length[a]	18.1 (16.3 –20.6)	16.7 (15.3 –18.2)	77
Prepostorbital	9.88 (8.78–10.1)	9.27 (8.61–10.7)	76
Pelvic origin[a]	44.1 (40.8 –47.4)	43.1 (40.8 –45.2)	75
Head length[a]	19.6 (18.1 –21.0)	18.9 (17.3 –21.0)	72
Head depth	13.8 (12.5 –14.9)	13.2 (11.9 –14.9)	72

[a] Adjusted to fork length 270 mm to allow for allometry.
[b] Spawning run samples (10 fish) omitted.

In searching for support (independent of gill rakers) for the contention that Squanga Lake fish are morphologically distinguishable into two forms, characters should not be used which are clearly correlated with gill raker count. Every character listed in Table II was found to show no correlation with gill raker number within the range of either low or high count forms. Of all characters examined, only gill raker length was correlated with gill raker count in such a way that bimodality in the former might be attributable to bimodality in the latter. Raker length was therefore omitted from further consideration, even though rakers in the high count form were, on the average, distinctly longer than in the low count form.

Another source of potential error in comparing characters of the low and high count forms is allometric growth of body parts coupled with different average size of the two forms. Almost all fish sampled for morphological study were between 200 and 350 mm fork length, but low count fish averaged longer than

high count fish. Therefore all measurements were plotted against fork length to discover those characters whose proportion changed with size. Those which did not were expressed directly as percent of fork length in Table II.

Pectoral length and body depth showed positive allometry in both forms (rate of increase of part greater than rate of increase of body length); pelvic origin and head length showed negative allometry in the high count form; head length showed positive allometry in the low count form. For these characters, each measurement was converted to the corresponding value on a fish of 270 mm fork length, using for conversion the slope of the line of best fit from a log–log plot of that part against fork length for all specimens of the corresponding form. These adjusted measurements are also expressed in Table II as percent fork length.

Sexual dimorphism was slight enough to be neglected in all characters in Table II except body depth. Females had somewhat deeper bodies than males in June; in November ripe females had much deeper bodies, and spent females had much shallower bodies than males. Spawning run samples were therefore excluded from calculations of body depth in Table II, and given intermediate values for body depth in calculating character index.

With the foregoing adjustments, six of the characters in Table II showed higher values for the low count form, and one (body depth) was lower. Figure 6 shows diagrammatically these and other mean differences in "average" 270 mm specimens of the two forms. Despite these average differences it was not possible even after handling hundreds of specimens to assign a fish with certainty to low or high count form before examining the gill rakers.

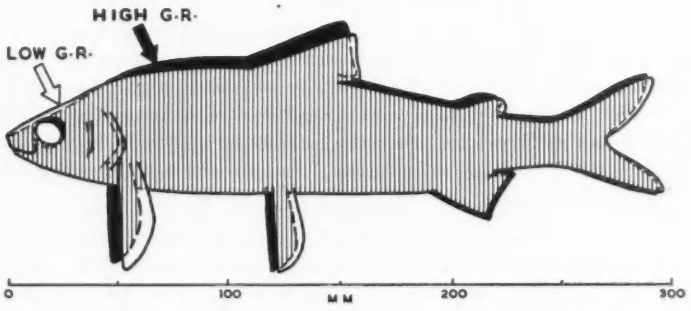

FIG. 6. Superimposed outlines of fish with high (27 or more) gill raker count (black) and low (26 or fewer) gill raker count (white). Dimensions are average for fish with fork length 270 mm. Based in part on data in Table II.

No significant differences between the two forms were found in counts of lateral line scales, scales above or below the lateral line, scales around the caudal peduncle, dorsal fin rays or anal fin rays.

Utility in "correctly" classifying specimens into low or high count form, according to whether they lay above or below an empirically chosen value for

each morphological character, is shown by a column in Table II. The best character, pectoral origin, classified 81% of the fish in agreement with their gill raker count; the poorest correctly classified 72%; other less useful characters are omitted.

All characters in Table II were combined to form a "character index" for each fish. Although the characters were not correlated with gill raker count, graphical inspection showed them to be partially correlated between one another. Pectoral origin, prepostorbital and head length formed one set of apparent partial correlations, and pectoral length was partially correlated with head depth. Despite such partial correlations, each of the seven characters was found by trial and error to contribute to separation based on a multiple character index. Certain other characters which were very closely correlated with some character in Table II were excluded because they were found not to enhance the separation.

To calculate the character index, the range of measurements for each character was divided in ten so as to include nearly equal numbers of individuals in each tenth. A score of from 1 to 10 was assigned each individual according to which tenth it occupied, the direction of the scale for each character being chosen with high end corresponding to fish with high gill raker counts. The character index for each fish was the sum of scores assigned for each of the seven characters in Table II. Hence, the maximum score of 70 would be attained by a fish whose every character lay amongst the 10% of fish closest to the high raker form with respect to that character.

A plot of the resultant character index against gill raker count (Fig. 7) shows that 90% of the fish either had high character index (above 34) and high gill raker count (26 or more), or else low index and low raker count. *Within* either high or low count halves of Fig. 7, there was no suggestion of correlation between character index and raker count. Therefore characters *independent* of gill raker number have been combined to produce a separation which agrees, for all but 10% of the fish, with separation based on raker count alone. Moreover, fish from the November spawning run (solid circles in Fig. 7), which fell exclusively within the high raker group, also fell exclusively within the group with high character index.

The few fish which do not conform to the general pattern in Fig. 7 are significant biologically. One fish with high raker count (29) nevertheless resembled the low raker form in 6 of 7 other characters, and hence had a very low character index. Similarly, a few fish with low raker counts resembled the high raker form in several characters and received a high index. The 4 markedly aberrant fish in Fig. 7 all were males; the one with 29 rakers had one gonad white and the other dark brown. The possible hybrid nature of these disjunct fish is discussed later.

Calculation of the character index used here was mathematically crude, in that characters of somewhat different effectiveness for separation were given equal weight, and no allowance was made for correlation between characters. Discriminant function analysis, conveniently carried out with an electronic

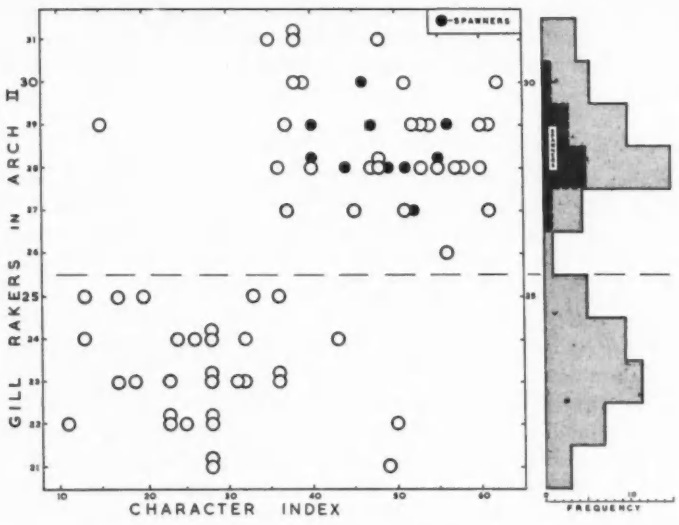

FIG. 7. Character index (calculated from 7 body proportions) and second arch gill raker count. Frequency distribution of the latter shown in histogram at right. Based on stratified sample corresponding to frequencies of first arch gill raker counts in surface samples in Fig. 2.

computer, is a more elegant technique which has been applied successfully on similar taxonomic problems (e.g. McPhail, 1961). In this case the technique would probably permit discrimination of a somewhat higher proportion of the sample, but it would probably not contribute further biological information; in the few disjunct individuals discussed previously no method of combining the morphological characters can disguise the fact that they do not have gill raker counts which would be expected from examining the rest of the sample.

DISCUSSION

SUMMARY OF EVIDENCE FOR TWO SPECIES IN SQUANGA LAKE

The two forms of whitefish in Squanga Lake behave as distinct species according to several lines of evidence. In fish taken over deep water, clear bimodality occurs in number of rakers in the first gill arch. A stratified sample of these shows almost complete separation into two groups on the basis of rakers on the second arch. Seven other morphological characters, each independent of gill raker count, can be combined to separate most individuals in conformity with the separation based on raker count. Spawning run samples in early winter contained exclusively fish with high raker count; these fish fell exclusively into the corresponding group on the basis of other morphological characters. Average depth distribution of the two forms in June was different. Differences

in stomach contents indicated divergence in feeding habits. Gonad development in June differed markedly and suggested difference in spawning time. Apparent hybrids were rare, indicating that little successful interbreeding occurs between the two forms.

Literature on Comparable Whitefish Studies

Lindström and Nilsson (1962) recorded differences in feeding, more carefully than in the present study, in sympatric whitefish species in Sweden. Wide divergence in diet was demonstrated, but differences in gill raker counts were great (modes of 21 and 46 in one lake; 19, 34 and 44 in another). Other morphological differences were not treated. Svärdson (1953) recorded sympatric pairs with gill raker modes as close as 20 *versus* 25 (Lake Idsjön) or 21 *versus* 27 (Lake Störsjon); these pairs differed in growth rate, but he did not record differences in feeding habits or morphology. Kennedy (1943) found two sympatric forms of whitefish in Lake Opeongo, Ontario, with gill raker modes of 25 and 27. No difference was found in relative size of 6 body parts, nor scale count, but the form with fewer gill rakers grew more slowly. Vertical distribution differed only in one month, August, when the "dwarfs" were concentrated in slightly deeper water. Feeding was not shown to differ.

Phenotypic Versus Genotypic Differences

Svärdson (1957) has summarized the arguments that gill raker count in whitefishes is almost unaffected by environmental influences. While his extensive studies have shown that gill raker count is far less subject to phenotypic modification than are other morphological characters, gill rakers should not be regarded as wholly unchangeable. Five transplants of whitefish in Sweden produced offspring in the new environment with gill rakers significantly different ($P < 0.001$) from their parents (Svärdson, 1952). Maximum differences were less than 2 rakers. More strikingly, Koelz (1929; p. 539) gave gill raker counts of thirty specimens of *Coregonus clupeaformis* reared all their lives in cativity; their gill raker counts (mode 25, range 23 to 28) lay well below those of their parental stock from Lake Erie (mode 28, range 25 to 30 (Koelz, 1931)) and below those of all Great Lakes samples combined. These fish, grown in the New York Public Aquarium, were drastically modified in appearance so as to resemble the broad whitefish *Coregonus nasus*, yet they maintained the gill raker *length* characteristic of the humpback whitefishes (Lindsey, 1962).

Gill raker counts are evidently subject to some phenotypic change, but then only over a relatively small range and only as a result of environmental influences likely to produce pronounced changes in other characters. Therefore, the difference of 4 or 5 between modal gill raker counts in the two Squanga Lake forms, unaccompanied by any striking differences in other morphological characters, can scarcely be attributed to environmental differences during development. If this be accepted, no case can be made for the two Squanga Lake forms having a purely phenotypic origin. If the gill raker differences are largely genetic, then it follows from the evidence summarized above that the forms are fulfilling all

generally accepted criteria for two good species. (This is not to say that *some* of the morphological differences are not phenotypic, nor that *some* of the behavioural differences may not be learned, perhaps in conjunction with a strong schooling tendency.)

Isolating Mechanisms

The presence of a few apparent hybrids raises the question "If occasional interbreeding occurs, what prevents the two populations from merging completely within a few generations?" It might be argued that fish whose gill raker counts disagree with their other characters are not hybrids, but merely represent extremes in variability within one or other species. Frequency distributions of both types of character argue against this. Moreover, Svärdson also found several lakes to contain occasional hybrids, distinguishable by gill raker counts intermediate between widely differing parental species.

Strong selection against hybrids because of poor adaptation, for example to feeding on specialized diet, seems unlikely. Niches of the two species in Squanga Lake apparently overlap widely, as does their morphology. Presence of adult hybrid fish suggests that hybrids are not all removed by selection before reaching maturity. Therefore ecological selection, although it may reduce the number of hybrids, does not totally eliminate them.

Hybrids may be sterile even though viable. However, several artificial crossings between whitefish species have produced viable offspring, and mass hybridization (introgression) seems to occur in some Swedish lakes (Svärdson, 1958). Hence the offspring of hybrids are probably sometimes also fertile. Hybrid fertility may, however, be much reduced. Also, behaviour of hybrids at spawning time may reduce their reproductive success.

So many situations have been found with two slightly overlapping but not identical sympatric whitefish species, that it seems unlikely that each has by coincidence been studied during the process of a rapid fusion between formerly discrete species. Probably the distribution of morphological types in Squanga Lake represents a balance, with ecological selection and differential reproductive success keeping gene flow between the species minimal but not blocking it altogether. In different lakes the point of balance may vary between complete segregation and mass hybridization, depending on diversity of habitats, competitors, predators, spawning sites, etc. Apparently the two remain separate in Little Squanga Lake as well as in Squanga Lake; there is some suggestion (Fig. 2) of an intermediate form in Summit Lake, but data are inadequate for decision. The possibility of intermediacy in other parts of the Yukon River system is touched on later.

The sympatric development of such a pair of species cannot be visualized, because genetic swamping in the initial stages would prevent divergence of the incipient species. The more likely hypothesis, of allopatric development of the two forms now sharing Squanga Lake (one coming from the Yukon basin glacial refugium and one from south of the Wisconsin ice sheet) is consistent with geographic distribution of gill raker counts elsewhere in North America.

NOMENCLATURE

Clarification of the taxonomy of the humpback whitefishes cannot come without much more extensive and intensive studies, within and between the Old World and the New. Binomial nomenclature may in the end be proved to be inappropriate. Designation of names for the species in Squanga Lake is therefore only tentative. At present, I believe that the form with modal gill raker count of 23 should be called *Coregonus pidschian*, corresponding in North America to fish in Bristol Bay drainages, Kuskokwim River, Chuckchee Sea drainages of Alaska, and perhaps the Alsek River, all of which areas have modal counts from about 20 to 23. The form in Squanga Lake with gill raker mode of 28 should probably be called *Coregonus clupeaformis*, a species occurring (with modes from about 26 to 28, possibly higher) eastward across the Northwest Territories and south to central British Columbia and the Great Lakes.

A form with modal count of about 25 occupies much of the Yukon River including Teslin Lake, and perhaps the delta of the Mackenzie River. This has been named *Coregonus nelsonii*, based on specimens from Nulato on the Yukon River (see Lindsey, 1963, regarding gill raker count). Perhaps *C. pidschian* and *C. clupeaformis*, which are able to remain separate in some lakes such as Squanga, frequently hybridize to form "*C. nelsonii*" in most of the Yukon River. Perhaps, on the other hand, *C. nelsonii* is a valid species which will be found to occur sympatrically with another humpback whitefish. Perhaps, in fact, neither of the two kinds of fish in Squanga Lake correspond to the species which have been suggested. One of the suggested species was named from a locality 2200 miles to the southeast and the other from 4400 miles to the westward. Information is so inadequate that little weight should be placed on nomenclatural bridges attempting to cross the intervening gaps.

ACKNOWLEDGMENTS

This study has depended on the cooperative efforts of many persons. Most of the field data and specimens were collected by Messrs E. D. Lane and the late A. W. Beadell. Dr T. G. Northcote kindly provided limnological data and soundings of Squanga Lake, and was assisted by Game Warden Barry Paull. Fisheries Officer W. K. Elliott obtained winter samples of spawning fish. Mr E. R. Combs of Squanga Lake helped in many ways. Mr J. D. McPhail assisted in collecting specimens both in 1958 and 1960. Dr W. B. Scott enabled me to examine specimens in the Royal Ontario Museum. Valuable criticisms of the manuscript have been offered by Drs N. J. Wilimovsky, P. A. Larkin and T. G Northcote. The assistance of all these persons is gratefully acknowledged, as is a grant from the President's Committee on Research, University of British Columbia.

REFERENCES

DYMOND, J. R. 1943. The coregonine fishes of northwestern Canada. *Trans. Royal Canadian Inst.*, **24**(2): 171–232. (*Contrib. Roy. Ontario Mus. Zool.*, No. 24.)

KENNEDY, W. A. 1943. The whitefish, *Coregonus clupeaformis* (Mitchill) of Lake Opeongo, Algonquin Park, Ontario. *Univ. Toronto Stud., Biol. Ser.*, No. 51; Publ. Ontario Fish. Res. Lab., No. 62, pp. 23–66.

KOELZ, W. 1929. Coregonid fishes of the Great Lakes. *Bull. U.S. Bur. Fish.*, **43**(2): 297–643. (Document No. 1048).

1931. The Coregonid fishes of northeastern America. *Papers Michigan Acad. Sci., Arts and Letters*, **13**: 303–432.

LINDSEY, C. C. 1962. Distinctions between the broad whitefish, *Coregonus nasus*, and other North American whitefishes. *J. Fish. Res. Bd. Canada*, **19**(4): 687–714.

1963 (in press). Status of the whitefish species *Coregonus nelsonii*, and designation of a new type. *Copeia*.

LINDSTRÖM, T. AND N.-A. NILSSON. 1962. On the competition between whitefish species. Pages 326–340 *in*: The exploitation of natural animal populations. Edited by E. D. LeCren and M. W. Holdgate. British Ecol. Soc., Symp. No. 2. Blackwell, Oxford.

MCPHAIL, J. D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. *J. Fish. Res. Bd. Canada*, **18**(5): 793–816.

MUNDIE, J. H. 1959. The diurnal activity of the larger invertebrates at the surface of Lac La Ronge, Saskatchewan. *Canadian J. Zool.*, **37**(6): 945–956.

NORTHCOTE, T. G., AND P. A. LARKIN. 1956. Indices of productivity in British Columbia lakes. *J. Fish. Res. Bd. Canada*, **13**(4): 515–540.

SVÄRDSON, G. 1952. The Coregonid problem. IV. The significance of scales and gill rakers. *Fish. Bd. Sweden, Inst. Freshwater Res. Drottningholm, Rept.* No. 33, pp. 204–232.

1953. The Coregonid problem. V. Sympatric whitefish species of the lakes Idsjön, Storsjön and Hornavan. *Ibid., Rept.* No. 34, pp. 141–166.

1957. The Coregonid problem. VI. The Palearctic species and their intergrades. *Ibid., Rept.* No. 38, pp. 267–356.

1958. Interspecific hybrid populations in *Coregonus*. *Uppsala Universitets Årsskrift*, **6**: 231–239.

WALTERS, V. 1955. Fishes of western Arctic America and eastern Arctic Siberia. *Bull. Amer. Mus. Nat. Hist.*, **106**(5): 255–368.

WYNNE-EDWARDS, V. C. 1952. Freshwater vertebrates of the Arctic and Subarctic. *Bull. Fish. Res. Bd. Canada*, No. 94, 28 pp.

Observations on Behavior of Juvenile Brown Trout in a Stream Aquarium During Winter and Spring[1]

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ABSTRACT

Observations were carried out in February–March and May–June periods during which water temperature ranges were 0.0–0.5°C and 8.5–12.5°C, respectively. Responses of fish to structures representing simplified environmental features, e.g. visual reference points, support against which fish could brace themselves in current, areas of slow water, overhead cover and areas of shade, were studied at three different water velocities. Winter and spring responses to illuminated and dark cover and to areas of rocky bottom were compared. Fish associated progressively more with experimental structures as more environmental features were incorporated into them. Degree of association with such structures and with other types of cover was much greater during winter. Degree of association increased with water velocity during both spring and winter. Increasing water velocities modified aggressive behavior. Fish displayed relatively more at low water velocities and nipped more at high velocities. It is possible that the association with and defence of specific locations on the bottom of a stream has selective value that alternates seasonally, providing the species with protection from predation and from displacement by current in winter, and with an efficient mode of food utilization in spring and summer.

INTRODUCTION

Seasonal changes in such environmental features as light, food supply or temperature may necessitate adjustments in the behavior of fish. In addition, internal changes related to age may be manifested in changes in the activity of a group of fish during consecutive seasons (Stringer and Hoar, 1955; McInerney, 1961; Northcote, 1958). In situations where marked seasonal environmental changes occur, adaptive changes in behavior and activity of animals may be anticipated.

Lotic environments impose special problems on the animals within them. Fish in streams are required to maintain position in the face of a constantly moving medium. Maintenance of position requires active swimming against the current in open water or a strong tendency to rest at or near one location on the stream bottom. Changing seasonal conditions, particularly water temperature, which would affect the metabolic demands of fish (Brown, 1957), as well as ability to perform activities (Brett *et al.*, 1958), may alter the general behavior of fish within streams.

A series of observations was made on the winter and late spring behavior of a group of yearling brown trout in a stream tank. Certain features of territorialism, aggressive behavior and attraction to the bottom were compared during winter and spring.

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MATERIALS

The investigation was carried out during February, March, May and June in the stream aquarium at the Hölle Laboratory in Sweden. For a description of the aquarium see Lindroth (1954).

A section of the main aquarium, 75 cm wide and 550 cm long, was used. The floor and the wall opposite the window in the tank were lined with masonite and painted a uniform grey. The tank was lit by nine 100-watt bulbs suspended at 55-cm intervals down the center of the tank 75 cm above the bottom.

Fish used in the experiment were all from the same hatchery stock of *Salmo trutta* Linnaeus. Those used for winter observations were from 5.3 to 6.8 cm in fork length (mean 6.3) while those used during spring were 6.2 to 8.4 cm (mean 7.4). Details of light and temperature history of fish used are unknown. However, fish used during winter were probably subjected to 8 or 9 hours of light, the period in which hatchery staff was present. By May the period of

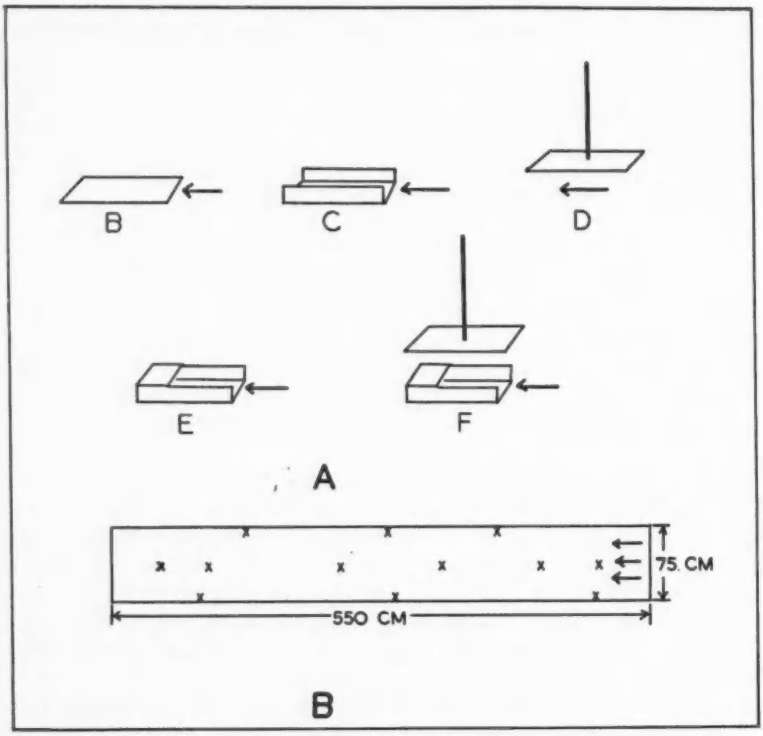

FIG. 1. **A.** Structures B to F used to modify bottom of stream tank. No objects were used on fish in control group A. Arrow denotes direction of current. **B.** Outline of bottom of stream tank with crosses indicating positions where structures were placed with each group of fish.

natural light would be increased to 16 or 18 hours. The water temperatures in the hatchery from which the fish were obtained were roughly comparable to those where experiments were carried out.

OUTLINE OF STUDY

Three experiments were carried out in February and March and were repeated during May and June.

I. Response to Patterns and Structures on the Bottom

The distribution and behavior of groups of 20 fish were studied in six different situations (Group A–F). Fish in group A were observed in an unmodified aquarium (bare floor) at 3 different water velocities: 8–9, 18–19, and 28–30 cm/sec. Fish in groups B to F were subjected to the same water velocities as those in group A. In each successive group, lots of 12 similar structures were placed at fixed locations on the floor of the tank (Fig. 1). The series of experimental structures were intended to combine different types of environmental features and reference points. An attempt was made to combine progressively more features from group A, the unmodified tank, to group F, which combined 6 environmental features (See Fig. 1). Flat black plates used in group B provide distinct strong visual reference points. Plates with sides turned up (group C) provide visual reference points plus lateral support. Overhead plates used in group D provide shade and overhead visual reference points. Boxes in group E provide visual reference, lateral support, direct support and areas of low water velocity. Table I lists types of environmental features and indicates how these were combined in experimental structures used in each group.

Table I. Features incorporated in experimental structures in groups B to F. Group A was used as a control.

	GROUP					
Environmental feature	A	B	C	D	E	F
Visual reference on bottom	–	X	X	–	X	X
Lateral support	–	–	X	–	X	X
Visual reference overhead	–	–	–	X	–	X
Shade	–	–	–	X	–	X
Direct support	–	–	–	–	X	X
Area of low current	–	–	–	–	X	X

The following procedure was repeated with each group of fish. Structures were placed in position and the water level was raised to about 28 cm in the tank. A group of 20 fish was placed in the middle portion of the tank and left in still water for 30 minutes. The water velocity was then increased over a 30-min period to the desired level and the fish were left for another 30 min. Follow-

ing this, records of positions of all fish were made at each 15- or 30-min interval over a period of 7 or 8 hr. At the same time the number of fish swimming free of the bottom was recorded. Periodic records were made of the number of nips and displays in the downstream $\frac{2}{3}$ of the tank during a measured time interval. Fish were fed midway during each series of observations. Following each series of observations at one water velocity, the water velocity was raised over a 30-min period to the next desired level and the observations were repeated over a second 7- or 8-hr period.

The positions of fish along the tank were determined by using a series of markers 25 cm apart below the window on the outside of the tank. Positions of fish across the bottom were estimated. Tests, in which locations of suspended "dummy fish" were estimated and then measured, indicated that such estimates could be made without serious error.

The room in which the observer worked beside the aquarium was kept unlit. Careful movements along the windows of the tank did not disturb the fish

II. Response to Opaque and Transparent Cover

Fish were offered a choice of two shelters which were identical except that one was black and opaque and the other was transparent. The shelters were 30- by 30-cm squares of plexiglass with the downstream edge elevated and enclosed to provide an area where current was reduced or absent. Fish could enter and leave the shelters via openings at the back and sides. An open side of the shelter was placed against the window of the aquarium so that the behavior of the fish could readily be observed in the opaque as well as the transparent shelter. One shelter was placed in the upstream end of the tank and the other in the downstream end. After a complete set of observations the positions were alternated.

During each set of observations a group of 40 fish was placed in still water in the tank and left for about half an hour. The velocity of the water was then increased stepwise from 10 to 60 cm/sec over 5 or 6 hr. Positions of fish, numbers under shelter, and aggressive behavior were recorded at 15-min intervals.

III. Response to Shelter Offered by Rocky Bottom

A 200-cm section of the downstream end of the tank was covered with stones 2 to 30 cm in diameter. The water in the tank, upstream from the area of stones, was about twice as deep as the water over the stones. As a result water velocities were always about twice as great over the stones.

Forty fish were introduced upstream from the stones while the water velocity was near zero. The water velocity over the stones was increased stepwise from 8 to 66 cm/sec. In this period the number of fish over the stone area, the number hiding among the stones and the number resting on the stones was recorded.

Water temperatures in the aquarium ranged from 0.0 to 0.5°C during February and March. During the spring experimental period (May 30–June 15) the water temperature increased gradually from 8.5 to 12.5°C.

RESPONSE TO PATTERNS AND STRUCTURES ON THE BOTTOM

Environmental Behavior

Figures 2, 3 and 4 are composite distributions of lots of 20 fish observed 20 times under winter conditions at water velocities of 8–9, 18–19 and 28–30 cm/sec, respectively. In each figure Group A represents the control situation and Groups B to F represent observations made with various structures on the floor of the tank. Figures 5, 6 and 7 are distributions of fish observed under spring conditions at water velocities of 8–9, 18–19 and 28–30 cm/sec, respectively. The tendency of one fish to remain at one location, or preference of different fish for a single location, is indicated by a cluster of dots.

Figures 2 to 7 demonstrate effect on fish distribution brought about by: (1) modifications of the bottom of the tank; (2) changes in water velocity; (3) changes related to season, i.e. light, age of fish and water temperature.

Increased complexity of the objects, groups B to F in Fig. 2–7, resulted in increased occupancy of the 12 stations where objects were located. This, in general, held true at each water velocity. At water velocities of 28–30 cm/sec, relatively fewer of the locations under structures in group D were occupied. Structures (group D) near the wall were occupied more readily than those in the center.

Increase in water velocity resulted generally in more fish being associated with the experimental structures (groups B, C and E of Fig. 2–4). No increase in tendency to associate with the structures in group F is apparent with increase in water velocity (Fig. 2–4), because structures were virtually 100% occupied in all cases. Structures or combinations of structures offering support or protection from current were extensively occupied at high velocities. Fish always occupied specific positions with regard to such structures. Stations were chosen such that the tail could be supported in the box or such that the fish were in the small region of still water downstream from the box (Fig. 6, 7). At higher water velocities fish not occupying structures showed a strong tendency to rest against the window of the tank, presumably as a result of differences in light conditions between the window and painted wall.

The wall, which was painted grey, reflected some light; the window, on the other hand, appeared dark from inside the aquarium.

Comparison of distributions of fish in winter (Fig. 2–4), with distributions at corresponding water velocities in spring (Fig. 5–7), reveals a much stronger response to structures during winter conditions. This seasonal difference is most evident at low water velocities (Fig. 2, 5).

In almost all cases the response to structures is weaker in spring than in winter. Figure 8 summarizes total numbers of cases in which individual fish associated with experimental objects in 20 observations on each group.

If a fish was on the object, under it, or with its head 8.5 cm upstream or downstream from the structure, it was considered to be associated with it. The figure 8.5 cm was chosen rather arbitrarily; however, if fish showed any obvious tendency to associate with the structures they were generally within 8–10 cm

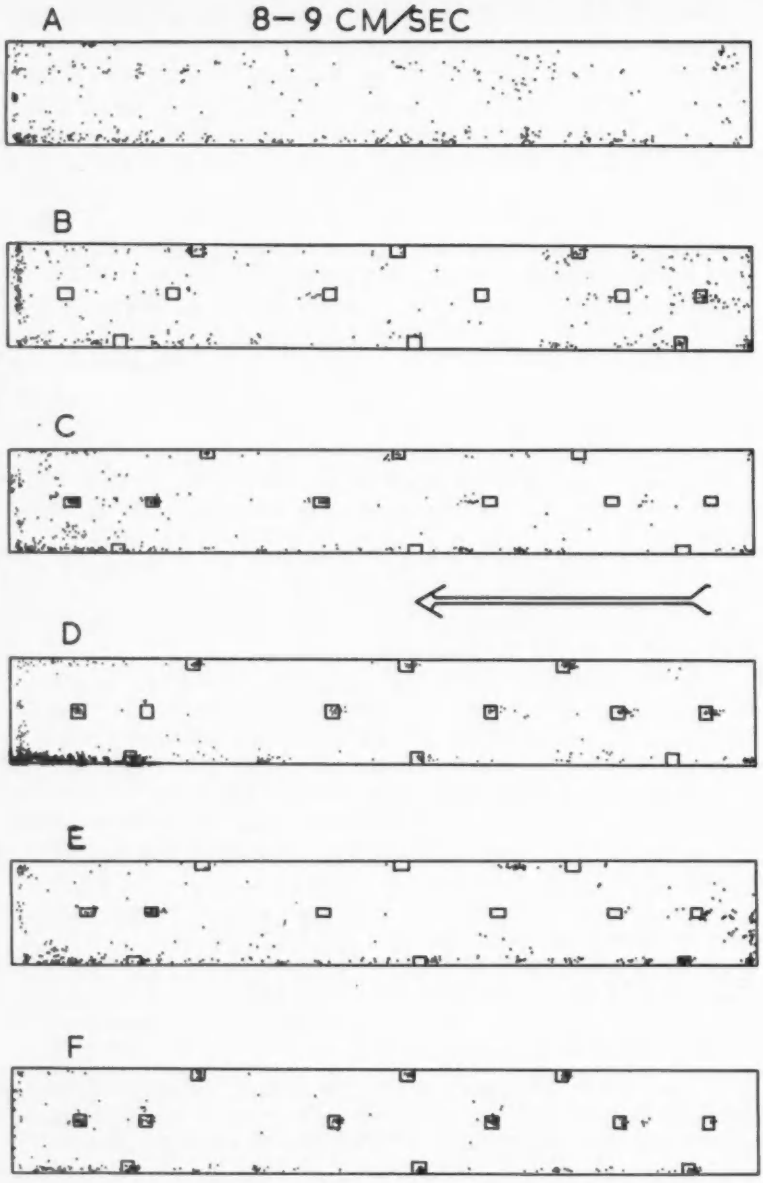

FIG. 2. Composite representation of distribution of 20 fish on 20 observations during February–March period. Water velocity 8–9 cm/sec, direction of current indicated by arrow. Water temperature range, 0.0–0.5°C. (See text for description of different structures used in A to F in Fig. 2–7.)

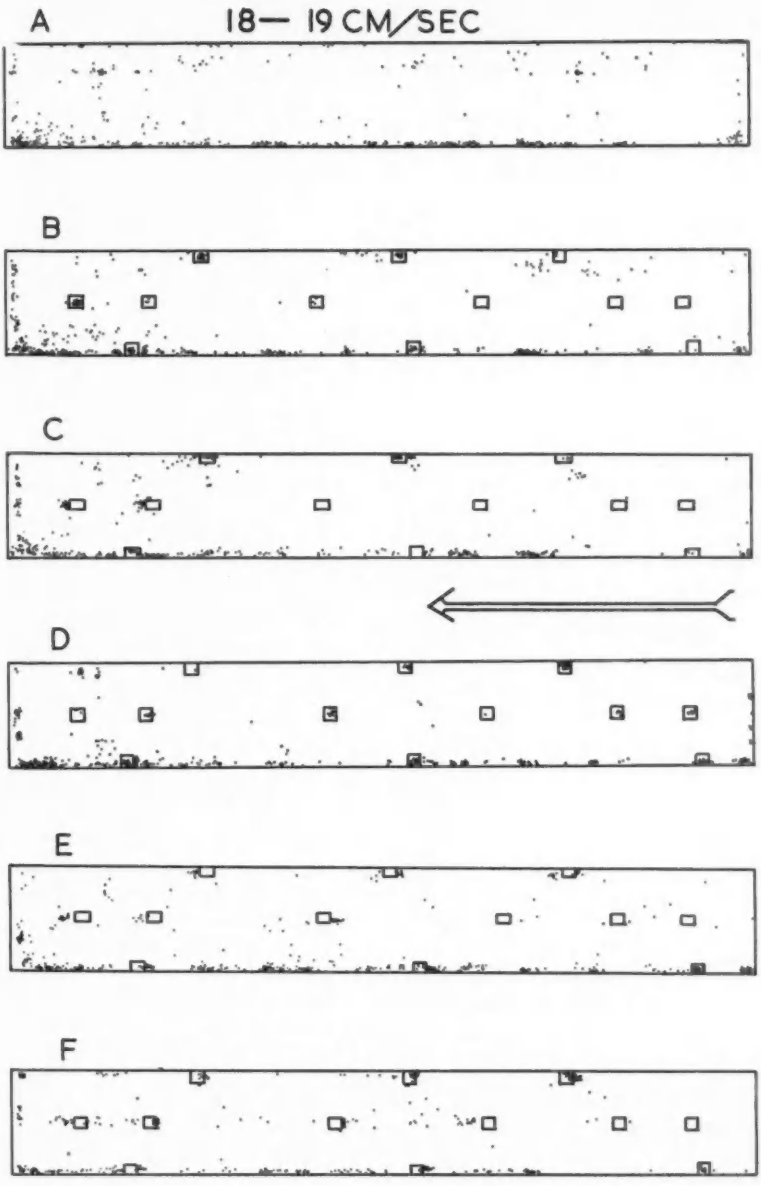

FIG. 3. Composite representation of distribution of 20 fish on 20 observations during February–March period. Water velocity 18–19 cm/sec, direction of current indicated by arrow. Water temperature range, 0.0–0.5°C.

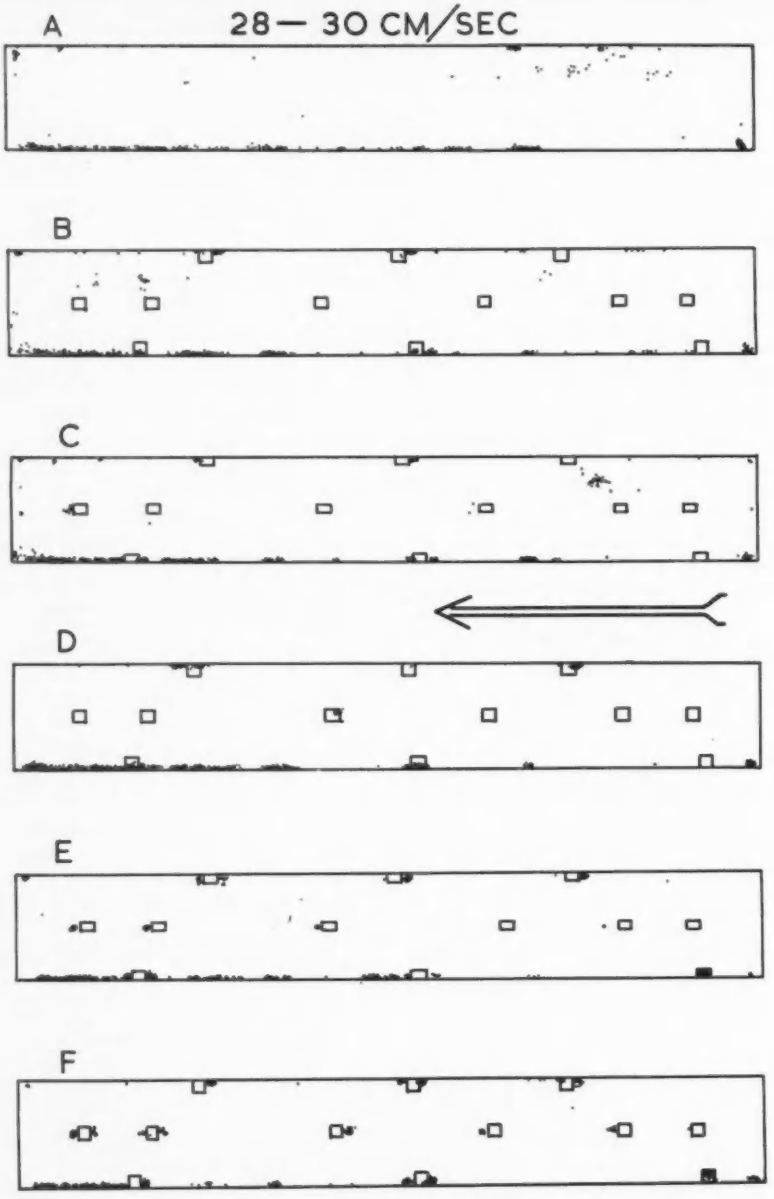

FIG. 4. Composite representation of distribution of 20 fish on 20 observations during February–March period. Water velocity 28–30 cm/sec, direction of current indicated by arrow. Water temperature range 0.0–0.5°C.

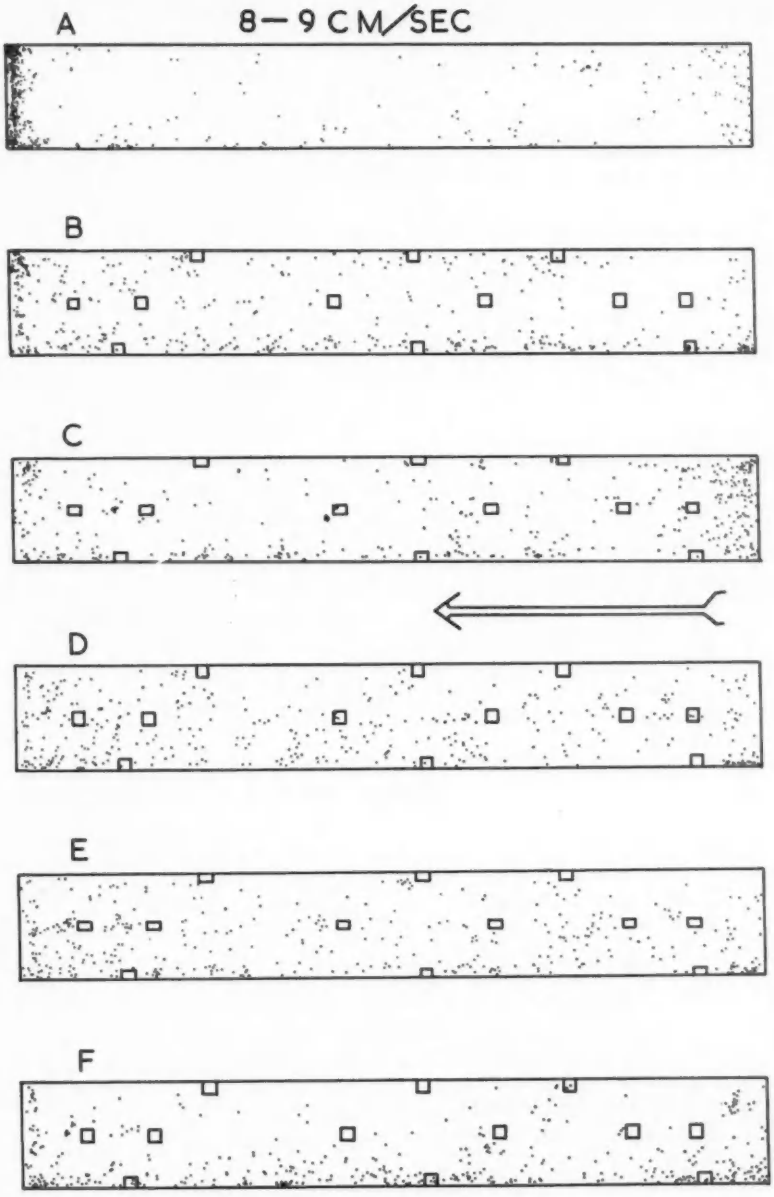

FIG. 5. Composite representation of distribution of 20 fish on 20 observations during May–June period. Water velocity 8–9 cm/sec, direction of current indicated by arrow. Water temperature range 8.5–11°C.

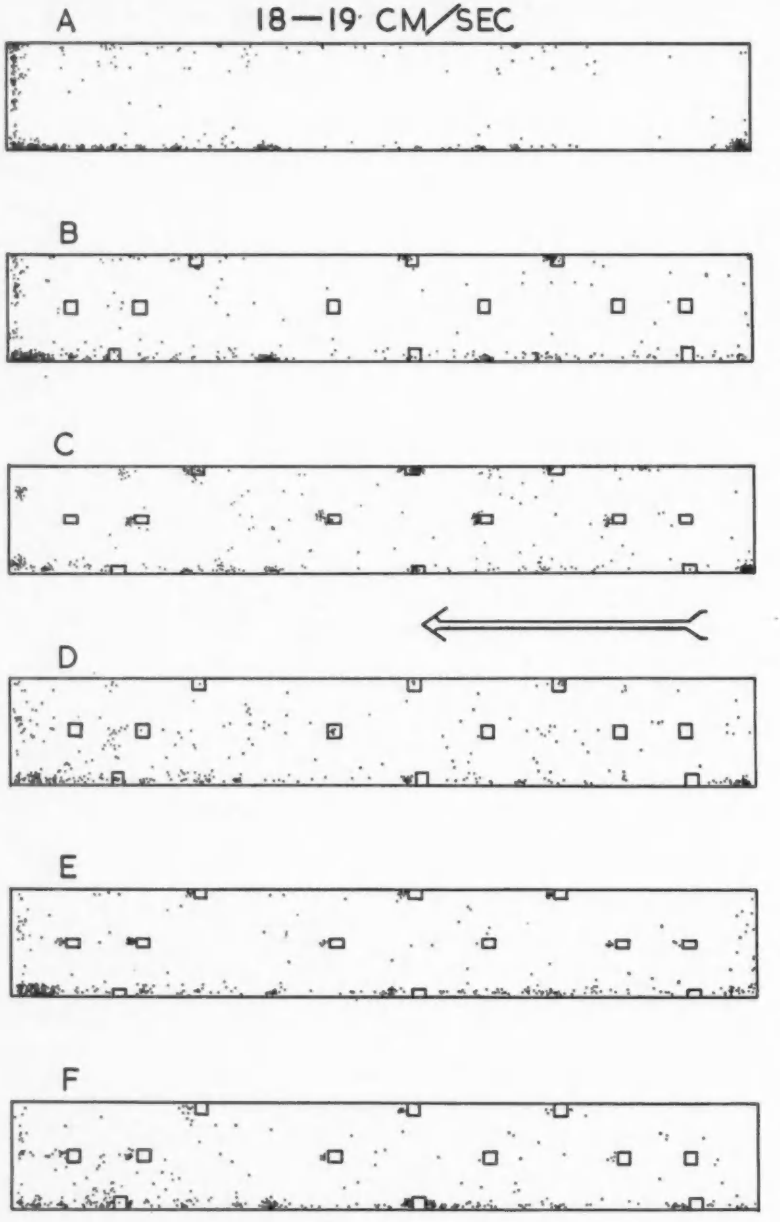

FIG. 6. Composite representation of distribution of 20 fish on 20 observations during May–June period. Water velocity 18–19 cm/sec, direction of current indicated by arrow. Water temperature range 8.5–11°C.

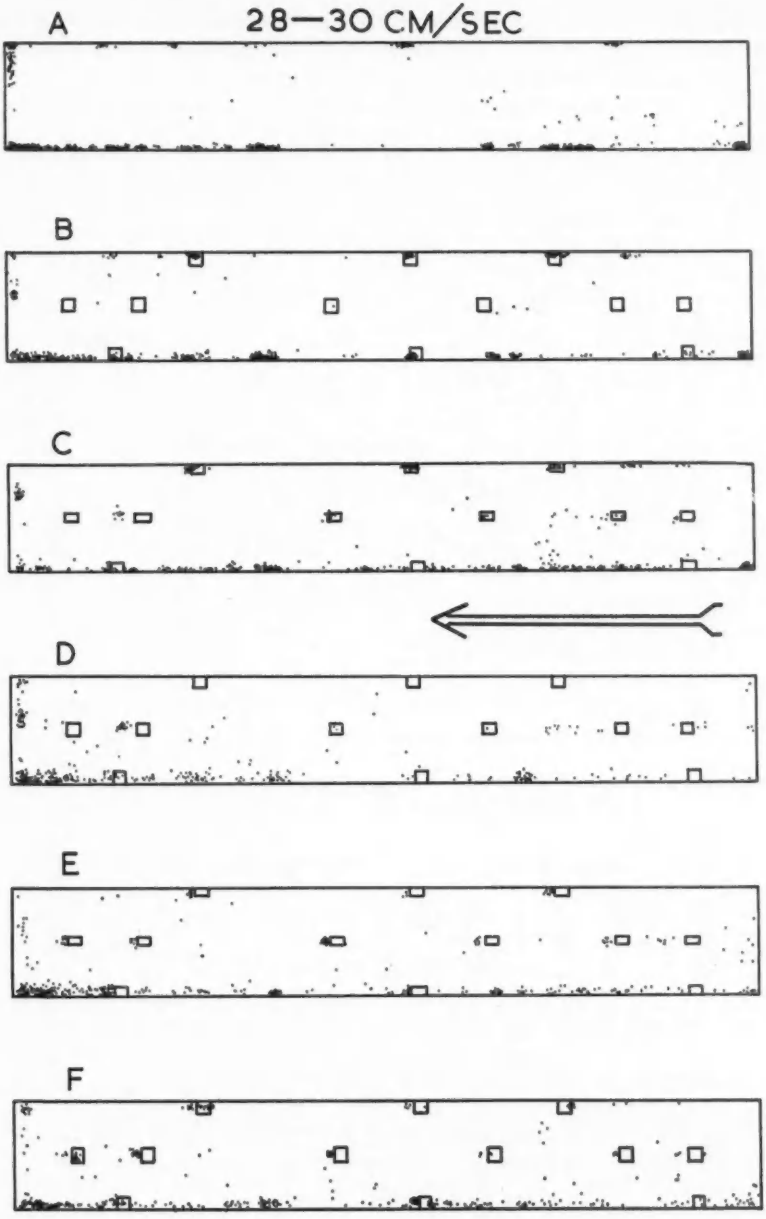

FIG. 7. Composite representation of distribution of 20 fish on 20 observations during May–June period. Water velocity 28–30 cm/sec, direction of current indicated by arrow. Water temperature range 8.5–11°C.

from them. Fish were not associated with the experimental structures at all at 8–9 cm/sec in the spring, but at 18–19 and 28–30 cm/sec there was some tendency, although less than in winter, to form such associations.

Figure 8 indicates that occupation of structures does not correspond as closely with increased complexity of structures in the spring as it does during winter. Fish showed less inclination to crowd into the corners along the sides of the aquarium in the spring. This difference in distribution was most clearly evident at water velocities of 28–30 cm/sec.

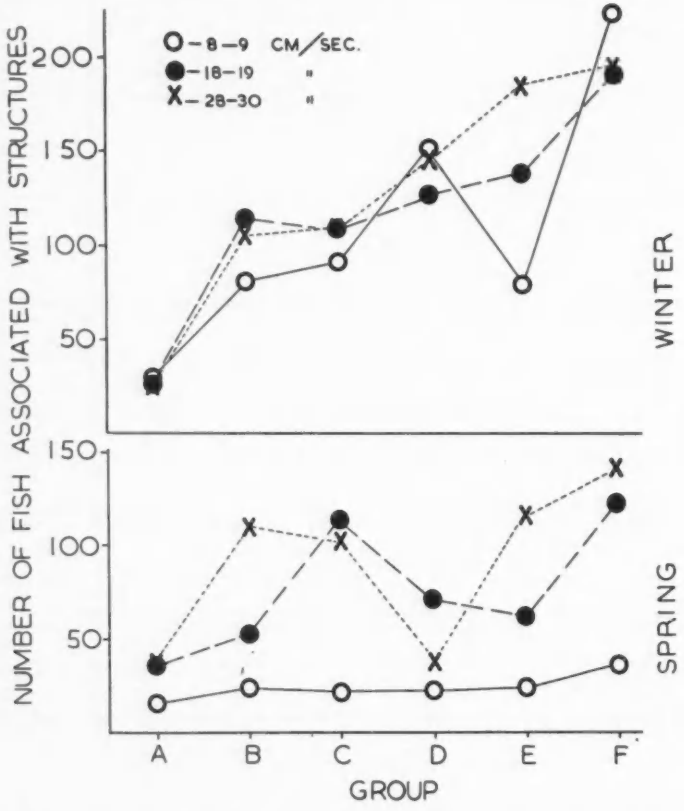

FIG. 8. Number of cases in which fish were associated with experimental structures in 20 observations on groups of 20 fish. Points in group A indicate the numbers of fish settling by chance on locations where structures were placed in groups B to F.

Fish observed in the winter generally remained at the bottom while in the spring most of them were off the bottom (Fig. 9). Data indicate that in winter the tendency to stay on the bottom was related to the amount of association

with structures placed there. Such a relationship did not exist in the spring. During both seasons the number of fish remaining at the bottom increased with higher water velocities.

Social Behavior

Aggressive behavior was recorded in two categories, nips and displays. Lateral and frontal displays described by Kalleberg (1958) were recorded together. Nips in which contact was made or in which contact was in doubt were all counted as nips. The classification and criteria used in recording agonistic behavior have the shortcoming that they do not quantify different intensities of display or attack. Since it was not possible to view the whole length of the aquarium

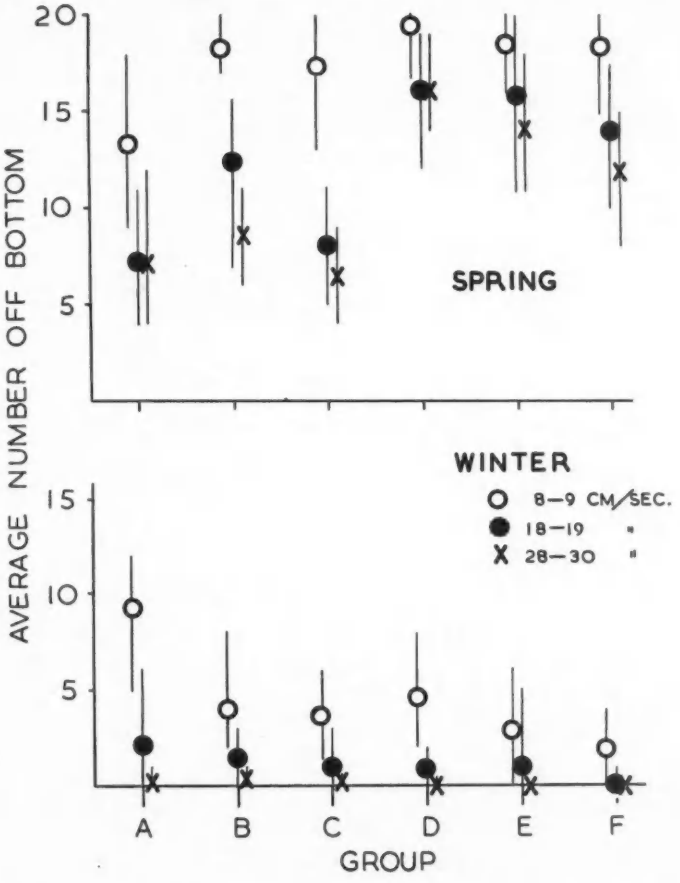

Fig. 9. Average number of fish off bottom of tank during winter and spring, 20 observations on each group at each of 3 water velocities. Ranges are indicated by vertical lines.

at once, social behavior was observed only in one-third or two-thirds of it at a time. Hence 6 to 16 of the total group of 20 fish were used in social behavior studies.

The amount and type of aggressive behavior observed was modified by feeding, and by changes in water velocity and differed in winter and spring. The rate of aggressive behavior, that is, combined rate of nipping and threaten-

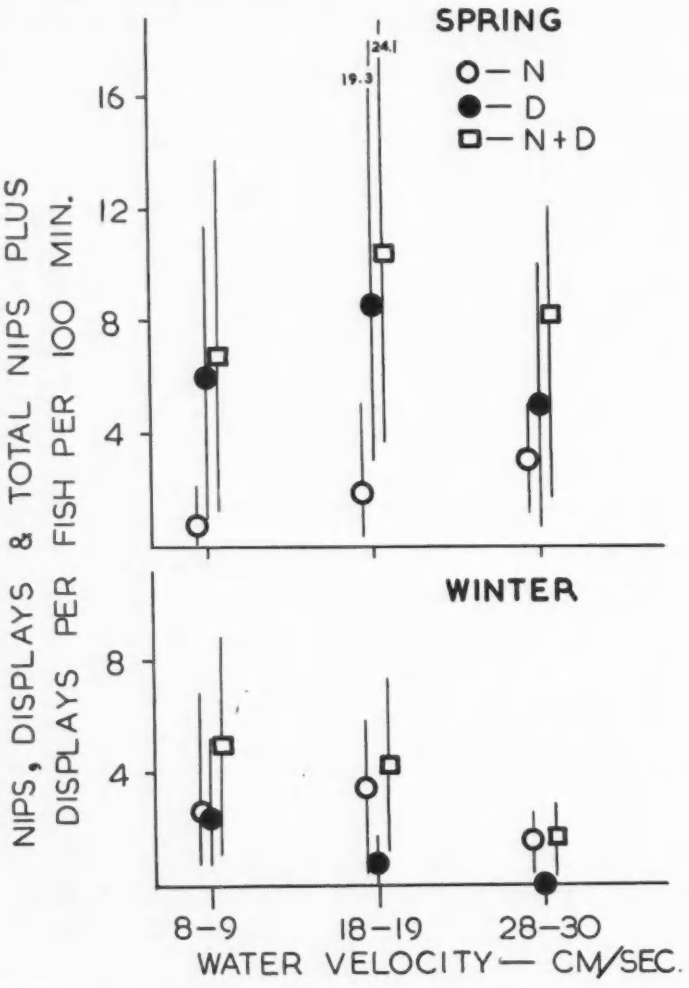

FIG. 10. Rates of aggressive behavior at three water velocities. N = Nipping; D = Displaying. Ranges indicated by vertical lines are based on combined observations on groups A to F for each water velocity.

ing per fish per unit of time, increased in 10 out of 15 cases after feeding in winter and in 14 out of 18 cases after feeding in spring. The rate of aggressive behavior decreased with increasing water velocity in the winter. Fish showed a higher level of aggressive activity (nipping and threatening combined) in the spring. In addition aggressive behavior was not reduced by increases in water velocity (Fig. 10). Displaying was more frequent during the spring than in the winter, but in both seasons the amount of displaying decreased, relative to nipping, with each increase in water velocity. Fish in display postures apparently had progressively more difficulty in holding position in the current with increasing water velocity. For this reason the intrusion of another fish was met more frequently with a quick bite.

Plots of data, not presented here, indicate that amount and type of aggressive behavior was unaffected by the type of structure used to modify the floor of the tank.

RESPONSE TO OPAQUE AND TRANSPARENT COVER

The numbers of fish hiding under dark and transparent cover, during comparable winter and spring conditions, increased with water velocity (Fig. 11). At comparable water velocities fish hid under dark cover more often than under

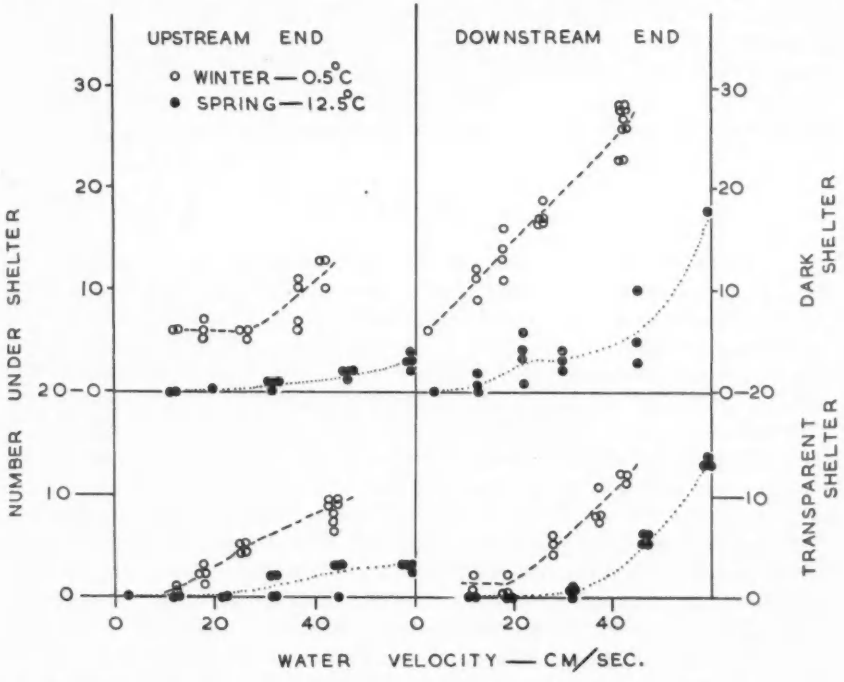

FIG. 11. Response to dark and transparent cover with increasing water velocity during winter and spring. Structures placed 75 cm from upstream and downstream ends. Each circle or dot refers to a single count of the number of fish under shelter.

transparent cover in winter. In addition, the hiding reaction to dark shelter began at lower water velocities. The observations hold true in the upstream end of the tank, where there was usually a smaller number of fish, as well as in the downstream end. During the spring fish showed much less response to either type of shelter than was shown in winter. Furthermore, in spring the fish showed no particular preference for dark shelter in either the upstream or downstream half. Under comparable current and shelter conditions the response was usually about 3 times stronger in the winter.

The amount of aggressive behavior under and around the shelters bore no apparent relation to numbers of fish, to season or to light conditions under the shelter.

RESPONSE TO SHELTER OFFERED BY ROCKY BOTTOM

Small trout, placed in the tank upstream from the area of stones, showed an initial tendency to remain in the deeper water. Increase in the water velocity resulted in progressively more fish being carried downstream onto the rocky area. A large increase in water velocity caused fish upstream from the stones to move to the corners of the tank and remain still. As a result only a limited portion of the 40 fish used moved over the stones (Fig. 12). An increasing number of these hid as water velocity was raised. At comparable water velocities the number of fish hiding was higher during the winter. The number remaining exposed to current above the stones was correspondingly lower.

DISCUSSION

Lindroth (1955) states that the habit of holding territories, among trout parr, is a reactive rather than a spontaneous behavior and that the release of this behavior is regulated and modified by conditions in the stream. The present experimental study indicates that rheotactic, visual and thigmotactic stimuli regulate in part the choice of stations and hence territories around them. The presence of distinct visual or tactile reference points and small regions of still or slowly-moving water induce a fish to take up a station in a given location more readily than if such reference points are absent. The observations indicate that if a relatively large number of small structures are scattered in the tank, a distribution and behavior, which has the essential features of territorialism, is obtained. Without such structures fish crowd along the walls of the tank, particularly at higher flows. Such distributions appeared less stable than those observed when environmental reference points were present. Fish placed in the stream tank with only two large structures offering cover, aggregated under such cover (Fig. 11). The observations suggest that fish in stretches of stream with uniform gravel bottoms are likely to be distributed in a territorial mosaic. Stretches of streams with scattered locations of good cover conditions might be expected to contain fish distributed in aggregations.

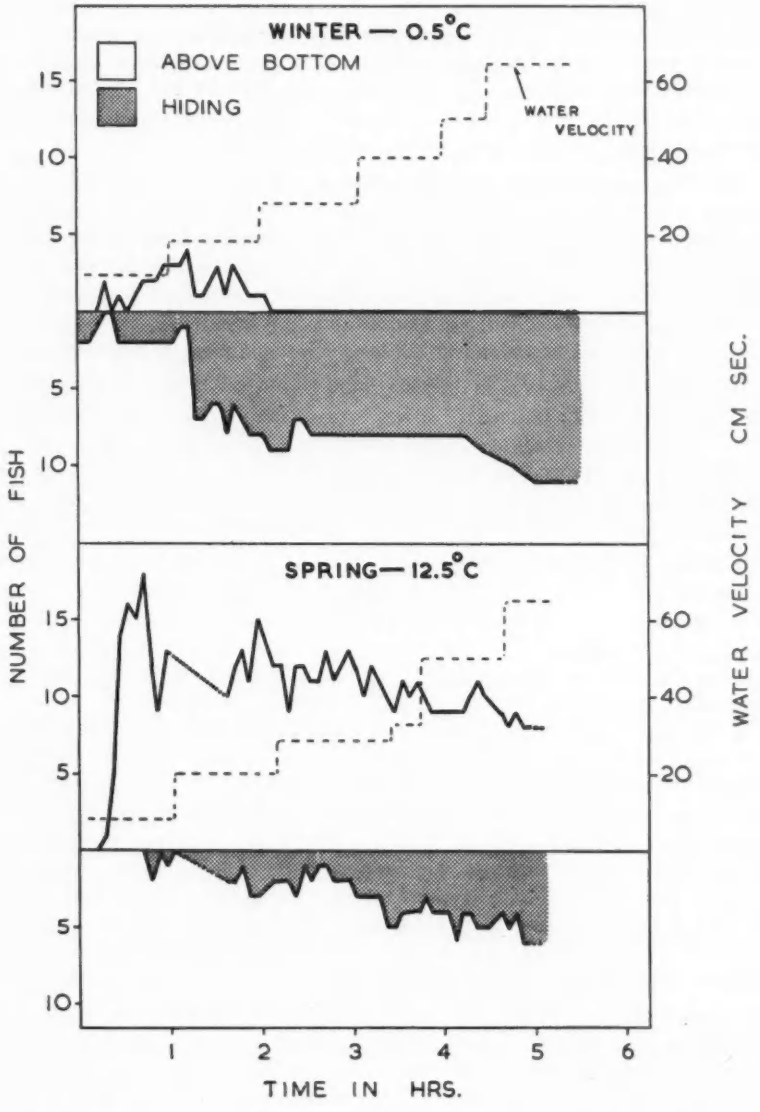

FIG. 12. Number of trout above the bottom, and number hiding among stones, with increasing water velocity.

Observations, particularly those made under winter conditions, indicate that fish in associating with experimental structures not only react to certain types of stimuli but also react in a manner that suggests summation of stimuli. The greatest reaction, or the strongest tendency to occupy stations, was noted where most stimuli were combined. This situation is similar, although perhaps not directly comparable to the situation where "heterogeneous summation" of environmental stimuli occurs among spawning fish (Fabricius, 1950).

The investigation does not indicate what conditions are responsible for the stronger association of small brown trout with the bottom during winter. Increased water velocity alone increases the tendency of fish to move to the bottom and occupy territories. Lower water temperature reduces swimming performance and produces essentially the same effect as speeding up the water velocity. Seasonal differences in performance occurred even though fish had been held at or near experimental temperatures and were acclimated to them.

The effect of differences in day length on the behavior of fish during winter and spring cannot be evaluated. It has been shown, however, that modification of day length alters current responses of rainbow trout (*Salmo gairdneri*) under controlled temperature conditions (Northcote, 1958). It is therefore possible that alterations in metabolism or behavior, as a result of differences in photoperiod, may have played a role in the seasonal differences observed.

Kalleberg (1958) states that the territories of juvenile salmon and trout are feeding territories. Trout observed in this study, under comparable flow conditions, showed stronger tendencies to remain at one location during the winter than during the summer. On the other hand, the amount of agonistic activity was lower during the winter (Fig. 10). Since food requirement and availability is probably lower during the winter a high degree of fixation to one location may be related more to other requirements than to feeding. Winter association with cover, shade and regions of low water velocity could be primarily a mechanism for gaining shelter and remaining in suitable reaches of stream over winter. Summer association with cover, shade and low water velocity, in one location, may serve primarily for efficient feeding. The strong tendency of the trout to hide readily among stones in the winter, and to avoid doing so to a great extent during the summer (Fig. 12), suggests an alternating seasonal emphasis on food and cover. The stronger attraction of winter fish to cover with low light intensity as well as to transparent cover (Fig. 11) demonstrates essentially the same reaction as the response to stone bottom.

Juvenile rainbow trout and coho salmon in coastal streams of British Columbia show a strong hiding response during winter. Investigation with diving equipment shows that, during winter months, hiding takes place among stones and under log jams. Fish in at least two age groups show this behavior, suggesting that it is caused by environmental conditions and is probably not related directly to age.

Certain general similarities in seasonal patterns of behavior exist in juvenile rainbow trout, brown trout and coho salmon. In each species seasonal changes

in behavior are such that the fish show stronger association with the bottom in winter than in summer. During winter such behavior affords protection against predation and displacement in the stream. Movement away from cover or emergence from the bottom in summer allows the fish to feed more when food (much of which is drifting in open water) is more abundant and when metabolism is such that more food can be used.

ACKNOWLEDGMENTS

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REFERENCES

Brett, J. R., M. Hollands and D. Alderdice. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Bd. Canada*, **15**(4): 587–605.

Brown, M. E. 1957. Experimental studies on growth. Pages 361–400 *in* Vol. I of The Physiology of Fishes. Academic Press Inc., New York.

Fabricius, E. 1950. Heterogeneous stimulus summation in the release of spawning activities in fish. *Rept. Inst. Freshwater Res. Drottningholm*, **31**: 57–99.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). *Rept. Inst. Freshwater Res. Drottningholm*, **39**: 55–98.

Lindroth, A. 1954. A stream tank at the Hölle Laboratory. *Rept. Inst. Freshwater Res. Drottningholm*, **35**: 113–117.

1955. Distribution, territorial behavior and movements of sea trout fry in the river Indalsälven. *Ibid.*, **36**: 104–119.

McInerney, J. E. MS, 1961. An experimental study of salinity preference and related migratory behavior of juvenile Pacific salmon. M.Sc. Thesis, Department of Zoology, University of British Columbia, 73 pp.

Northcote, T. G. 1958. Effect of photoperiodism on response of juvenile trout to water currents. *Nature*, **181**: 1283–1284.

Stringer, G. E., and W. S. Hoar. 1955. Aggressive behavior of under-yearling Kamloops trout. *Canadian J. Zool.*, **33**: 148–160.

Temperature, Salinity and Plankton in the Eastern North Atlantic and Coastal Waters of Britain, 1957. I. The Characterisation and Distribution of Surface Waters

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ABSTRACT

Monthly temperature-salinity diagrams for 1957 have demonstrated that three surface oceanic "water bodies" were consistently present in the eastern North Atlantic; two are regarded as modified North Atlantic Central water which give rise to the third by mixing. As well in the oceanic areas, large and small, high or low salinity patches of water were common. Effects of seasonal climatic fluctuations differed in the several oceanic water bodies. In coastal waters, differences in properties and in seasonal and annual cycles of the properties distinguish the waters from the North Sea, English Channel and the western entrance to the Channel.

The geographic distributions of the oceanic waters are consistent with "northern" and "southern" water bodies mixing to form a "transitional" water. Within this distribution there are short-term changes in boundaries and long-term (seasonal) changes in size of the water bodies.

Water in the western approaches to the English Channel appeared to be influenced chiefly by the mixed, oceanic transitional water; oceanic influences in the North Sea appear to have been from northern and transitional waters.

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INTRODUCTION

MONTHLY MEAN VALUES of surface temperatures and salinities in the North Atlantic and coastal waters of Britain have been produced in charts or atlases (Lumby, 1925; Anon., 1933, and Jacobsen, 1934; Anon. 1944; Smed, 1958). Investigations of surface waters in specific areas have been made, among others, by Helland-Hansen and Nansen (1926), Jacobsen and Jensen (1926), Tait (1937), Sverdrup *et al.* (1942), Corbin (1947), Cooper (1952), and Tulloch and Tait (1959). Yearly data are also available in the "Annales Biologiques" of the Conseil International pour l'Exploration de la Mer.

The above materials provide a background of temperature or salinity against which occurrences and distributions of organisms may be gauged in a general manner (Fraser, 1950, 1952, 1955). More specific relationships between occurrences of planktonic organisms and physical properties of their environment have been demonstrated by means of temperature-salinity-plankton (T-S-P) diagrams, (Pickford, 1946, 1952; Bary, 1959). In these, the presence and relative abundance of species are entered on the temperature-salinity (T-S) diagrams in the intercept of the temperature and salinity at each of the positions at which they were captured.

The aims of the present investigation were to determine whether water bodies of distinctive properties could be characterised for near-surface oceanic and coastal areas of the eastern North Atlantic and if so, whether species of zooplankton showed recognisable relationships to them. To this end temperatures and salinities between the surface and 5 m have been plotted in T-S diagrams after the manner of Miller (1950), Rochford (1957) and Bary (1959) for each of the 12 months of 1957. Water bodies are characterized and their geographic distributions are considered.

The occurrences of planktonic organisms in relation to the water bodies are dealt with in subsequent papers.

MATERIALS

The temperatures and salinities used in the present study are the majority of those collected during 1957 for the Bureau Hydrographique of the Conseil International pour l'Exploration de la Mer. The observations were made from a variety of commercial vessels and weather ships. Temperatures were taken via the condenser intake. They are corrected for variation in thermometers between ships and are tabulated for the Bureau in steps of 0.1° C. Salinities have been determined by British, French, Dutch and occasionally Norwegian laboratories; they are probably correct to ± 0.5 ‰.

In the North Sea, and along and across the English Channel, observations were made on regularly run routes. In the Atlantic, observations were dependent on sailings of weather ships to and from Weather Stations A, I, J, and K (Fig. 1). Schedules were sometimes spasmodic. A few lines of observations were run from the Bay of Biscay to Weather Stations A, J, or K, and to westward of K, chiefly by French vessels. The approximate locations of routes are shown in Fig. 1, and in detail in Plates VII to IX (*see also* John and Brown, 1958).

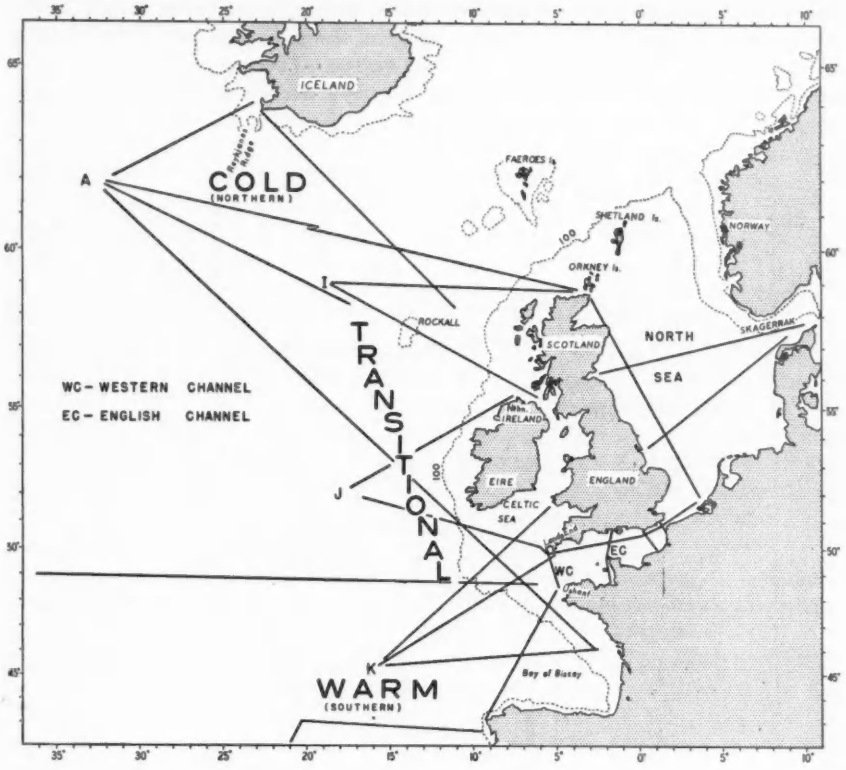

FIG. 1. Routes along which observations of temperature and salinity were collected during 1957. *A*, *I*, *J*, *K*: locations of Weather Stations; *cold*, *transitional* and *warm* refer to the general areas occupied by water bodies.

PROCEDURE

The temperature and salinity at a station determines its location in the T-S diagram. One station is "related" to others with similar properties so that a group of stations may be formed. Stations in a group represent some degree of homogeneity in the properties of the water in which they were located. These groups are the basis of the water bodies. They are delineated regardless of the effects of climate, latitude, or water movements, providing that the length of time covered by one diagram is reasonably brief, e.g. one month, and that the area surveyed is reasonably large.

When temperatures and salinities beyond about 100 miles from the edge of continental shelf were enclosed in straight-line envelopes, the form of the diagrams was similar to those shown in Fig. 2 and 3, and Plates I to VI. The addition of data from waters lying between the shelf-edge and 100 mi seawards altered

these diagrams in only minor details. When, on the other hand, data from the waters over the shelf were included, almost all the plotted points lay to the left of the envelope of the offshore (oceanic) water. These points, together with others from the North Sea and English Channel, constitute the coastal waters (Fig. 2).

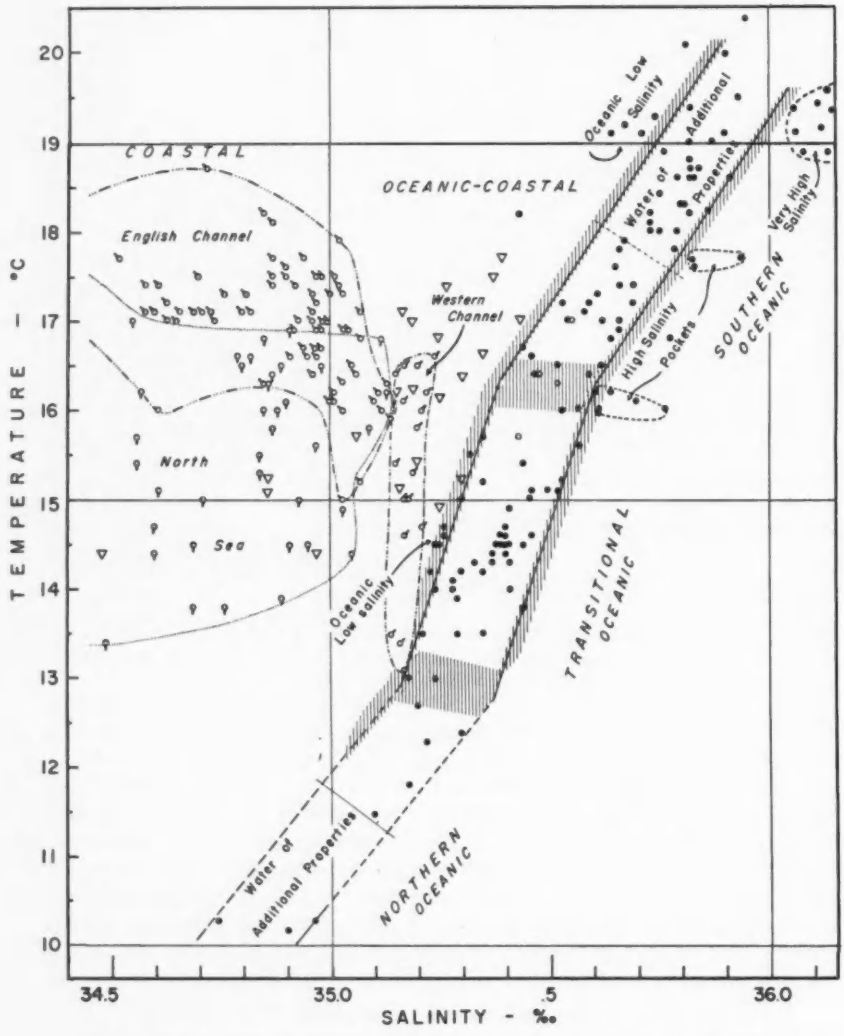

FIG. 2. A surface-water T-S diagram of the eastern North Atlantic and coastal waters of Britain. The names of the several "water bodies" are those used in the text. Zones of "immediate mixing" are shown by cross-hatching.

A few samples from the shelf fell within the oceanic water envelope (small open circles, Plates I to VI); these are regarded as oceanic water that has intruded onto the shelf.

North Sea, English Channel and Western Channel waters have been differentiated on the basis of observations made in particular areas. The North Sea (Fig. 1) is contained within the Strait of Dover, the Skagerrak and latitude 59° N approximately; the "English Channel" extends from the Strait of Dover to the vicinity of the line of stations between Land's End and Ushant (Ile d'Ouessant); the "Western Channel" was sampled only between Land's End and Ushant. Coastal waters in the Celtic Sea and along the west coasts of Eire and Scotland are not differentiated. Comparatively few observations were available and these are indicated in the T-S diagrams as inverted triangles.

Samples with salinities less than 34.1‰ were not plotted. The bulk of these resulted from outflow of dilute water from the Baltic into the North Sea.

The oceanic water envelope is angular and the angles are interpreted as demarcating "water bodies" since they indicate changes in properties. Three water bodies are apparent of which one is warm, one cold and the other has intermediate properties. These are referred to hereafter as northern, southern and transitional, respectively. Two narrow zones have been arbitrarily established between the northern and transitional and the southern and transitional water bodies. These are regarded as zones of "immediate mixing". They have been formed by adding together sections of an estimated one-tenth the length of each of the water-body envelopes which form the angles (Fig. 2).

Other zones of "immediate mixing" have been established along the lateral margins of the oceanic water envelope, between oceanic water and high or low salinity pockets, and between oceanic and coastal waters. When observations from any of these zones are presented geographically they are shown as occurring in "boundary zones" (Fig. 9) separating the oceanic water bodies from each other, or from the other waters. The boundary zones between oceanic water bodies indicate the limits to which unmixed northern or southern waters extend inwards, or conversely, the limits to which mixed transitional water extends outwards. Between oceanic and coastal waters the boundary zone indicates the shoreward limit of oceanic water that is unmixed with coastal waters.

An indispensable aid to the interpretation of data is a set of "working" T-S diagrams in which all points can be identified and cross-checked with the geographic locations of the stations. In these, consecutive observations along a route are joined by lines. The procedure enables relationships between adjoining stations or groups of stations to be demonstrated. At times these relationships have assisted interpretations and when this is so it is stated in the text. The "working" diagrams are too complicated to be reproduced.

TEMPERATURE-SALINITY DIAGRAMS

Oceanic Waters

Helland-Hansen and Nansen (1926) and Sverdrup *et al.* (1942, p. 669) have prepared T-S diagrams of the waters of the North Atlantic. The former used data from 1911, 1914, and 1922, collected north of about 32° N (off west

Africa), to Iceland, and between the edge of the European continental shelf to about 36° W. Sverdrup *et al.* plotted data from 10 selected stations representative of the North Atlantic. Helland-Hansen and Nansen differentiated samples from between 100 and 500 m, Sverdrup *et al.* a few from the surface and others from 100 m. Envelopes (Fig. 3) have been drawn about the points representing these shallow samples.

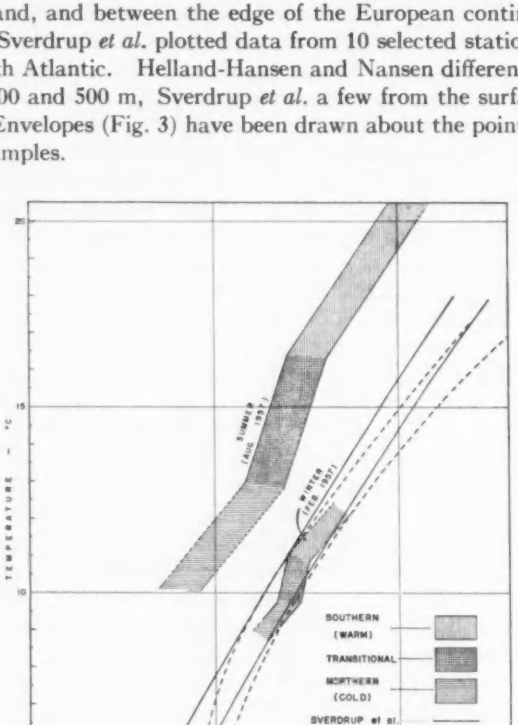

FIG. 3. T-S diagrams of sub-surface waters, after Helland-Hansen and Nansen (1926) and Sverdrup *et al.* (1942), compared with diagrams of surface waters for winter (February), and summer (August), of 1957.

Identical T-S diagrams probably could not be expected. However, the forms are similar and overall agreement is reasonable, especially between approximately 9 and 13° C. This portion of the diagrams conforms with the surface water T-S structure during the winter of 1957, probably as a result of effects of vertical mixing and winter cooling on the surface water properties. There is near conformity between the mean slope of the surface T-S diagram and the slopes of the diagrams of the deeper water. However, the diagram for oceanic surface waters is made up of three parts and in this it differs from the sub-surface diagrams. This structure was consistent despite seasonal fluctuations in properties, influences of extraneous waters and uncertainty in constructing diagrams in a few months.

The surface-water diagram is interpreted to show relatively unvarying relationships between the properties of three oceanic water bodies during 1957, in the eastern North Atlantic. On the other hand it probably is not indicative of the meeting and mixing of two different water masses. Helland-Hansen and Nansen's (1926) diagrams suggest there is a single body of water, westward of the area surveyed in the present study, which in moving eastwards, becomes divided into two branches. Modification of the waters in the branches probably ensues from the action of different climatic, and possibly also oceanographic factors, with the result that observations from them become separated. The cold water of low salinities (from the northern branch) has been named northern water and the warm, high-salinity water (from the southern branch), southern water. For the purposes of the present study these are considered "primary" oceanic water bodies which are contained within the North Atlantic Central water mass. Interaction between the two primary water bodies forms transitional water which has intermediate properties, less range of salinity and a steeper temperature gradient than either of the contributing waters.

High- and Low-Salinity Pockets

The surface T-S diagrams indicate that single or groups of observations from oceanic water often fell outside the oceanic-water envelope (Fig. 2). These were from either diluted or more saline water, relative to water of similar temperature within the envelope. Such observations were not always present.

The high salinities (points lying to the right of the envelope — Plates I to VI) on occasion exceeded the salinity of southern water by up to several parts per thousand. Notable examples occurred in November (Plate VI) when maximal values of 36.2‰ were obtained, and in October (Plate V) when they were above 36.4‰; maxima of 36.1‰ and 36.2‰ were present in May (Plate III), and 36.3‰ in July (Plate IV). Water with these salinities was also of relatively high temperatures; it has been named very-high-salinity water. There is no other water with properties of very-high-salinity water consistently represented in the diagrams so that it must originate in another source.

Upwelling Gibraltar water has been suggested as contributing relatively high-salinity water to the surface westward of Eire (Tulloch and Tait, 1957). Helland-Hansen and Nansen (1926) and Cooper (1952) have stated that the maximum salinity of the core of Gibraltar water, between 700 and 1000 m in the Bay of Biscay, lies between 35.7 and 35.8‰, at a temperature of about 9 to 10° C. Such are approximately the winter values of southern water (Fig. 3), but they were exceeded in the pockets of very-high-salinity water on several occasions. Thus a source other than upwelled Gibraltar water is required. Helland-Hansen and Nansen's diagrams suggest that water of suitably high salinities is located towards the Azores Islands.

Pockets of water of relatively high salinity, but of lower temperature than the very-high-salinity water, may have originated in the cooling of the latter. Alternatively, they may have resulted from intrusions of southern water, becoming detached and surrounded by a water of lower salinity.

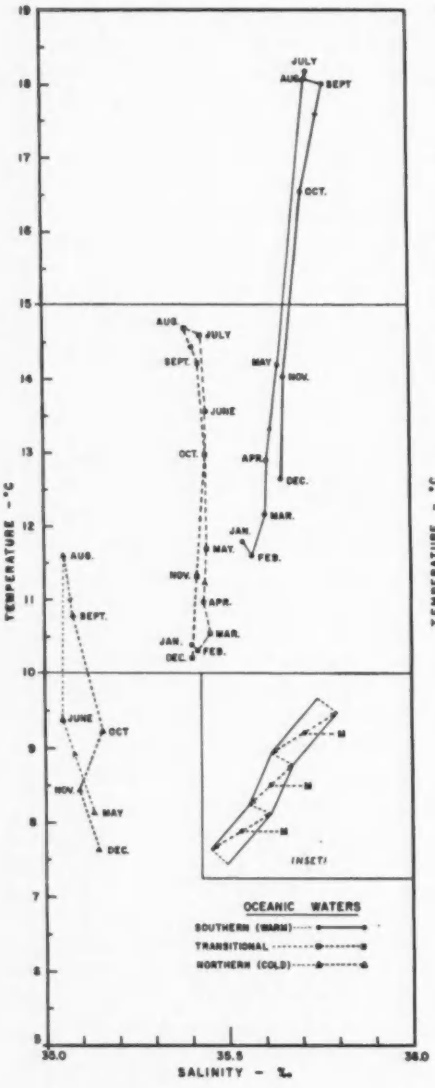

FIG. 4. Monthly means of surface temperatures and salinities for oceanic water bodies.

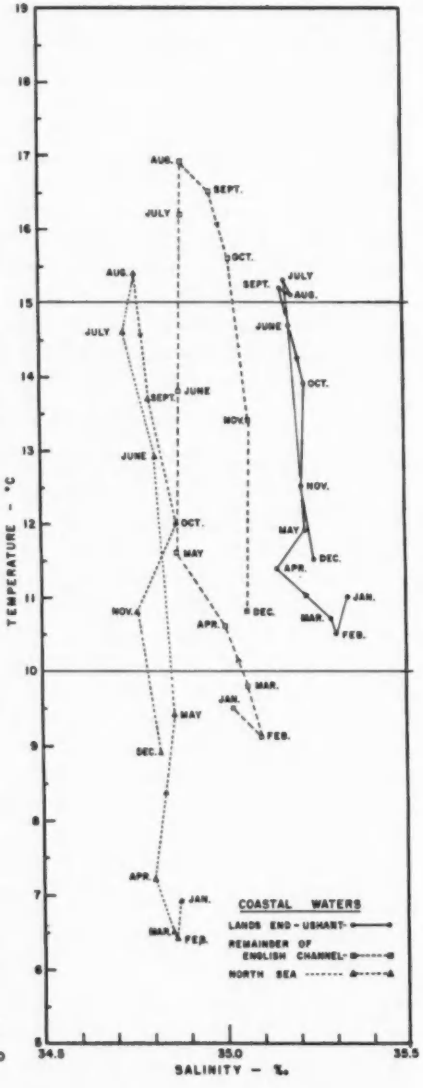

FIG. 5. Monthly means of surface temperatures and salinities for coastal water bodies.

Pockets of low-salinity water, relative to surrounding oceanic water, may have resulted from precipitation; this would probably apply at considerable distances beyond the shelf. Or low-salinity coastal water may have moved offshore. It could not be decided for particular pockets near the shelf which of these possibilities applied.

The T-S diagrams show that the pockets are a spasmodically recurring feature of the surface oceanic waters. Their properties vary which indicates either diversity of origin or of history. The very-high-salinity pockets suggest an influence of waters from beyond the area sampled; other pockets, of lower-salinity water, may have originated within the area surveyed from precipitation or other cause. Their presence adds complexity to the surface water structure.

The Seasonal Cycles and Ranges of Properties

The seasonal warming and cooling of the oceanic water bodies is illustrated in a general manner by the T-S diagrams (Plates I to VI). Southern and northern waters were not sampled adequately in several months and arithmetic means were not feasible. Instead, "diagonal means" were obtained from the mid-point of a line running diagonally across each water body (Fig. 4, Inset, *M*). This "mean" was not considered satisfactory for northern water from January to April. During these months its value was higher than in May and later months. The higher values resulted from the absence in the northern area of a cold water (see below, this section) which was present subsequent to May and lowered the monthly means. The available "mean" temperatures and salinities for the oceanic waters are plotted in Fig. 4. They illustrate the monthly sequence in the marine climate for each of the three oceanic water bodies characterised by the T-S diagrams. Figure 6 presents the annual temperature cycle, based on the diagonal means, for the oceanic waters and one coastal water body.

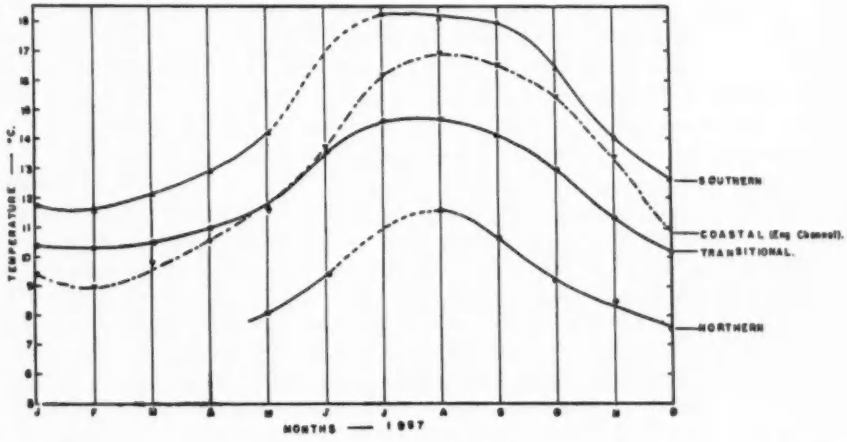

FIG. 6. The annual temperature cycles for the oceanic water bodies and the English Channel.

In the oceanic waters the temperature (Fig. 4, 6) increased slowly between February and April and then rapidly from May to July. The rate of decrease between August-September and December was less rapid and more uniform in all oceanic waters than the previous rate of increase. Both rates were higher, and the amplitude greater in southern than in northern water. Transitional water had intermediate values. These features are reflected in the annual ranges (Fig. 6).

The annual temperature range (Fig. 4, 6) was greatest in southern water; it was less in transitional water, and probably least in northern water, but data were lacking for the earlier months of the year. Maximal (mean) temperatures were attained during July or August in the three water bodies. The minimal temperature occurred in February in southern and transitional waters, but is not known for northern water for 1957. The values of the maxima and minima differed considerably between the water bodies.

During 1957 mean monthly salinities varied insignificantly in the oceanic water bodies, except for the first few months (Fig. 4), when irregular fluctuations occurred. Values generally were greatest for southern, least for northern water, and intermediate between these in transitional water. A progressive, lateral broadening of the water envelopes (Plates I to VI) with the approach of summer and a corresponding decrease during autumn and winter indicates that at any particular temperature, the salinity range increased during summer and decreased during winter.

Between winter and summer the temperature of the southern water body increased relative to that of the northern water body (Fig. 4, 6). An increase of the monthly temperature range of transitional water resulted, from 1.5 C° in January to 4 C° in August. During cooling the reverse occurred, so that the monthly range of temperature in transitional water fluctuated during the year.

In northern and southern waters the monthly temperature range presented a more complex situation. The T-S diagrams show that the envelope of southern water in July, and of northern water in May, suddenly increased in length. The feature is illustrated in Fig. 7. The ranges of temperature and salinity are shown by lines drawn from point "O", equivalent to $x - y$ (Inset, Fig. 7) for southern water, and $a - b$ for northern water.

In southern water, during five months (January to May) the range of temperature approximated 2 C°, and of salinity, 0.2‰, or less. There were no data for June, but by July, the temperature range had increased to better than 3 C°, and salinity to above 0.3‰. Thereafter the ranges continued to vary; maximal values occurred in August and September of 4 C° and 0.5‰. In northern water, from January to April, the monthly temperature range lay between 1.25 C° and 1.5 C°; the range of salinity was 0.2‰, or less. Maximal ranges of 5 C° and 0.6‰ were observed in June; during the remaining months values fluctuated. In southern water the monthly ranges increased as the result of a sudden increase in maximal salinities and temperatures; in northern water they increased because the minimal temperatures and salinities were

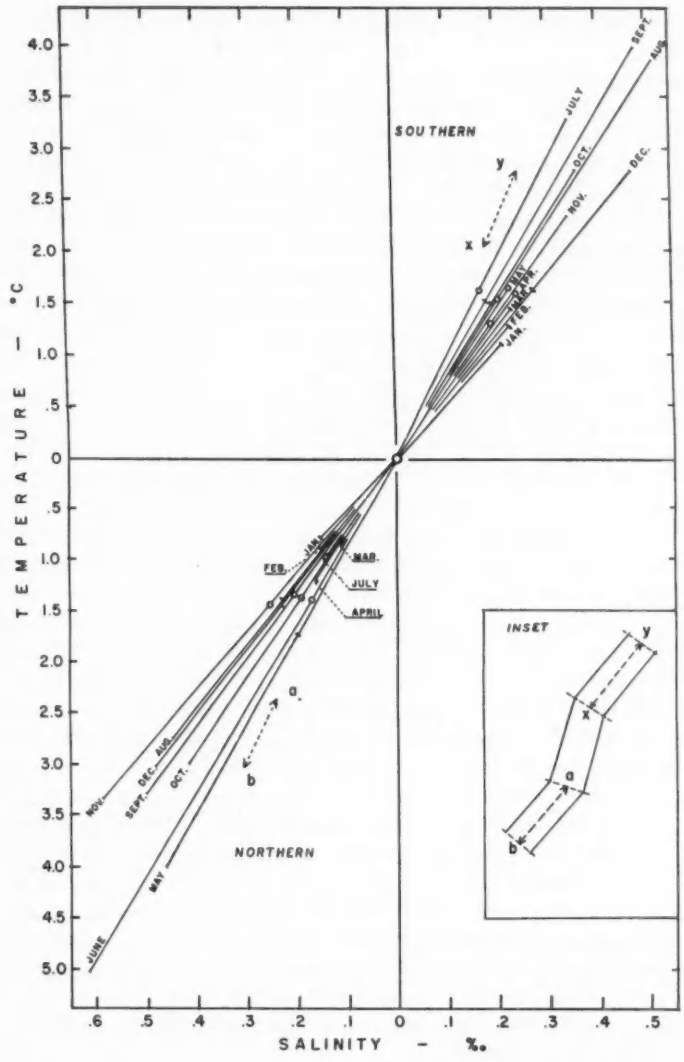

FIG. 7. Monthly ranges of temperature and salinity of northern and southern waters. *Inset:* T-S diagram of oceanic waters to indicate how the lines centred on O were obtained.

(—|—) The temperature at the transverse line (in the T-S diagrams) which marks either the position of an increased gradient preceding the occurrence of "water of additional properties", or the absence of this water. (—o—) As for the above, except that the position of the gradient is less certain.

suddenly lowered. The variations were concurrent, but opposed. The months of increased ranges coincide with the months of extended envelopes in the T-S diagrams.

The working diagrams showed that when increased ranges were present, steepened temperature gradients regularly occurred on passing from northern or southern waters into those "waters of additional properties" contributing to the increased ranges. When the gradients were obvious their approximate positions are indicated in the T-S diagrams with a fine, transverse line, and in Fig. 7 by a transverse dash; where several series of observations occurred in one diagram the positions of the gradients were sometimes less certain and are shown by dashed lines in the T-S diagrams and as open circles in Fig. 7. In several months, (January to April or May), a transverse line closes the ends of the envelopes of northern and southern waters. It indicates that no water of additional properties was sampled.

If the less certain data (Fig. 7) be accepted, there are reasonably close assemblages of points in both northern and southern waters which suggest that the monthly range of temperature throughout the year in either water was between 1.5 C° and 2.0 C°. Monthly salinities ranged from 0.25‰ (January) to less than 0.2‰ (July) in southern water and from 0.2 to 0.15‰ in northern water. It would seem from these data that, regardless of the seasonal cycles, there were narrow, "basic" monthly ranges of temperature and salinity in northern and southern waters.

These basic ranges should not preclude the possibility that some fluctuation of the range may have occurred. The present study indicates that any such fluctuation probably was small, and may not have exceeded 0.5 C°.

The temperatures and salinities of the waters which extended the envelopes in summer and autumn were additional to the basic range. Since the additional properties fitted the conformation of the T-S diagram without any noticeable hiatus in salinity it is probably unjustified to regard them as originating in distinct water bodies. They appear to arise in modified northern and southern waters. Climatic effects could not account for extensions to the water envelopes which were concurrent, but opposed.

In the geographic charts, (Plates VII to IX) the positions of the gradients and the water of additional properties are indicated. It is apparent that in northern areas the water of low temperatures and salinities was observed when sampling extended far enough into the northwest Atlantic, whereas in the south, the water of higher temperatures and salinities appears to have moved northward, into the area surveyed.

Neither the T-S diagram nor the charts (Plates VII to IX) indicate the origin of the waters of additional properties, nor reasons for their occurrences. They are interesting because they increase what appear to be a basic, narrow, monthly ranges of temperature and salinity in northern and southern waters. These increases will affect annual ranges by raising the monthly means in southern water, and lowering them in northern water. In transitional water, on the other hand, the monthly range increased during the summer because of differential

heating of northern and southern water bodies. The factors discussed constitute real differences in the temperature regimes of the several waters.

Coastal Waters

In the North Sea, English Channel and Western Channel, salinities of 35‰ and greater are considered to result when water of oceanic origin mixes with resident coastal water of lower salinity (Harvey, 1925; Carruthers, 1927; Russell, 1935; Tait, 1937). If these mixed waters have similar temperatures and salinities to an oceanic water from another area, the two will overlap in the T-S diagrams. This is apparent in January and February (Plate I) when English Channel and northern waters overlap. Waters with such similar properties in the T-S diagrams should be analysed in the context of the origins, and proximity to one another, of possible source waters.

In the North Sea (Plates I to VI), maximal salinities tended to be lower in April and from July to November (35.1 to 35.2‰) than from January to March, May, June, and perhaps December (35.2 to 35.3‰). In addition fewer stations were observed at the lower than at the higher salinities. It is probable these data indicate variation of the strength of the inflow into the North Sea. If so, it would seem that during 1957 there was a fairly strong inflow up to March, followed by a reduced flow in April; the flow possibly increased again in May and June, but from July to November it became progressively less. A further strengthening appeared to take place in December.

Large ranges of salinity in the North Sea and English Channel resulted from the influences of fresh and relatively high-salinity waters. For most of the year there was a limited monthly range of salinity in the Western Channel. Low values were present in April (34.4‰) and September (34.9‰). An influx of fresh water, such as Cooper (1960) described, or exchange of low-salinity water with the English Channel (Plates II, V and VI) may have caused this dilution.

Temperatures in the coastal waters are shown in Fig. 5 and 6; the points represent the arthmetic means of observations plotted in the T-S diagrams. Lowest winter temperatures occurred in all three waters in February and highest in August in the North Sea and English Channel, and in July–August in the Western Channel. Temperatures increased slightly between February and March and more rapidly during April and May, especially in the North Sea. Largest increases occurred in June and July in all waters. In Fig. 5, the monthly increments and decrements are seen to vary considerably between the three waters.

The annual temperature cycle and rate of change for coastal waters is ndicated by the curve for English Channel water (Fig. 6). The curve has a similar conformation to the equivalent curves for oceanic waters, but the amplitude of the seasonal change was greater in the Channel. The curve for the North Sea would be similar to that for the Channel, but again, of greater amplitude; in the Western Channel, however, the amplitude would approximate that for transitional water (Fig. 4, 5).

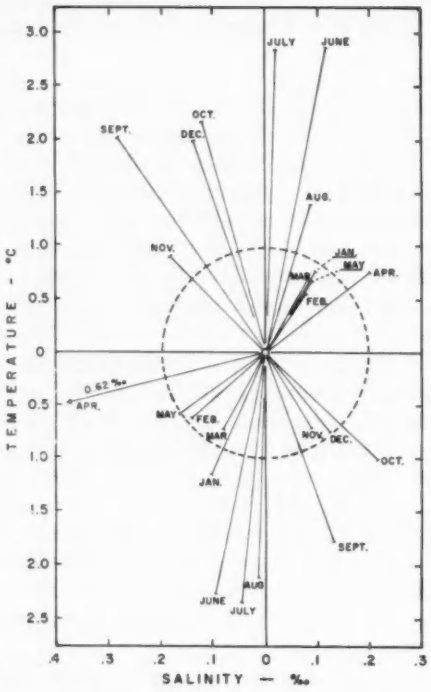

FIG. 8. Monthly ranges of temperature and salinity in water of the Western Channel. The zero position is equivalent to the calculated mean of temperature and salinity of the Western Channel water for each month; the lines for each month represent the range of the temperature and salinity above and below the mean value. The dashed circle represents a range of temperature of 2.0 C°.

The area of the western approaches to the English Channel is oceanographically complex (Lumby, 1925; Carruthers, 1927; Russell, 1935; Cooper, 1960a). Data from 1957 indicate various features of, and influences bearing on, the area. Temperatures and salinities in the Western Channel for the most part fell within a narrow range. The compact grouping of samples suggests relatively stable oceanographic conditions in the area.

For six months, from January to May and in November, the temperature range of Western Channel water varied between about 1.5 C° and 2.0 C° (Fig. 8). Between May and June the range increased to almost 5.5 C° and this continued into July; between August and December, ranges fluctuated between 2.5 C° and 4 C°.

The monthly range of approximately 2 C° from January to May and in November is similar to that in northern and southern waters. This range, coupled with the usually narrow salinity range (Fig. 5, 8), may result from oceanic water influences in the area, together with effects from cool, deep water being advected into the surface water. On the other hand, the relatively large fluctuations occurring at times appear to require additional warm and cool influences in the Western Channel. In September, October and December warm water could have originated in the English Channel where temperatures higher than in the Western Channel were being maintained (Fig. 4 and 5). In June maximal temperatures of the Western Channel were higher than in the English Channel and the warm water to have caused these must have originated elsewhere. Relatively cool water occurred (June, July, August; Plates III, IV and VIII), usually in the neighbourhood of Ushant, but also occasionally near Land's End. The low temperature of this water varied only slightly even though there was a general (seasonal) increase throughout the waters of the English and Western Channel. It may have resulted from local upwellings (Cooper, 1960).

From these considerations there seems little doubt that the waters of the three coastal areas were distinctive in 1957, despite the broad overlapping of properties illustrated in the T-S diagrams. Distinguishing features are the differing ranges of temperature and independent temperature regimes, and different mean monthly salinities. The Western Channel water proved less variable than the English Channel and North Sea waters, probably as a result of strong oceanic influences.

One general impression gained from Plates I to VI and Fig. 4 and 5 is that the properties of Western Channel water resembled those of transitional rather than those of southern or English Channel waters. In February, March, April, May and August (Plates I to VI), temperatures in the Western Channel were similar to, and maximal values did not exceed those of the warmest (southern) transitional water. In some later months, the maxima were higher than in transitional water, but warm-water influences from the English Channel, or elsewhere, were probable. Even so, the bulk of the plotted points usually were within the temperature range of transitional water. In Fig. 4 and 5, it is clear that the annual temperature ranges of Western Channel and transitional waters were similar; and that the mean salinity of the Western Channel water was intermediate between transitional and English Channel waters, and was less variable than the latter.

Differences between the mean monthly temperatures and salinities of southern and Western Channel waters were usually pronounced and suggest there was little direct exchange between them. In June and July, however (Plates III and IV), temperatures in the Western Channel were higher than in either the English Channel or transitional water and a warm water influence is indicated. This may have originated in southern water. No increase in salinity (Fig. 5) accompanied the increased temperature and it may be inferred that any such influence was attenuated, or indirect.

That the main oceanic influence in the Western Channel was from transitional water during much of 1957 seems a reasonable suggestion, but it may not have been strong at all times, or sustained. Increased temperatures and low salinities at a few stations from September to December indicated some influence from the English Channel; the high temperatures of June and July indicated a warm-water influence which may have originated in southern water. Relatively cool water during a few months, near Ushant and Land's End, possibly resulted from local upwelling.

GEOGRAPHIC CONSIDERATIONS

A generalised diagram of the distributions of water bodies is shown in Fig. 9. In the geographic presentation the water-body boundaries delimited in the T-S diagrams (Fig. 2) are "contoured". At times the boundaries coincided with the lines of samples, which may have resulted from inadequate coverage. It should be emphasized, however that to assign adjacent stations to the same or different water bodies in a geographic chart depends on whether their T-S properties cause them to be plotted in the same or different water bodies in the T-S diagram. The contours or boundaries are T-S lines; they are not equivalent to isotherms or isohalines. Their numerical values vary from month to month according as the limiting values of the water bodies in the T-S diagrams vary from the effects of climatic fluctuations. Where the geographic boundaries of a water body were estimated the lines are dashed instead of solid.

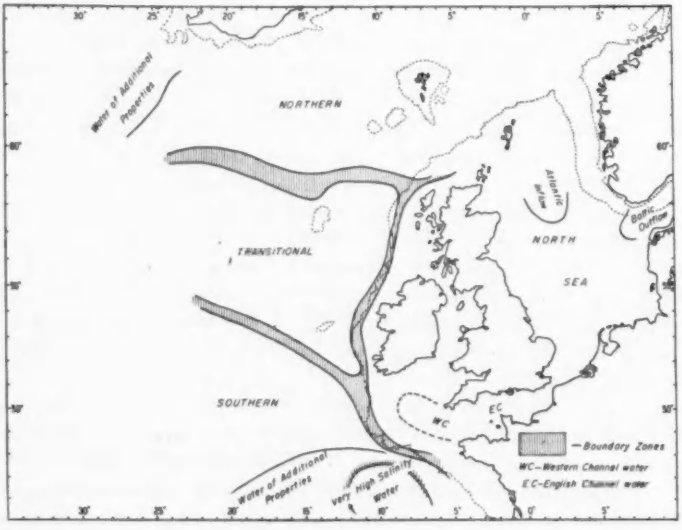

FIG. 9. Simplified diagram showing the general locations of water bodies. Boundary zones are cross-hatched and are equivalent to the zones of "immediate mixing" shown in Fig. 2.

General Distributions

Northern, southern and transitional waters

The geographic limits of the water bodies fluctuated during the year. The fluctuations fall into short- and long-term categories. Short-term changes lasted only a month or so; they involved smaller or larger alterations in the dispositions of "boundaries" between water bodies; incursions of extraneous waters are also in this category. Such changes were additional to the long-term ones. Long-term changes were manifest in progressive alterations in the size and to some extent the locations of the oceanic water bodies (Plates VII to IX).

From January to June or July, the southern boundary of northern water lay about due west from the northern tip of Scotland (59° N). It moved northwards during the summer and autumn, and developed large bulges. By December it again lay roughly east–west, but a little further to the north than in the previous January and February.

In January the northern boundary of southern water extended westwards in about the latitude of northern Ireland (55° N). From February to July the boundary moved southward until its shoreward end lay west of the Western Channel whence it ran roughly northwesterly into the Atlantic; it maintained approximately this position until October. In November it began to move northwards and by December it was again situated off northern Ireland. During the winter months therefore, relatively warm southern water penetrated further northward than in the summer. A southern boundary to southern water was present only when it was in juxtaposition with very-high-salinity water (January, February, July, October and November).

During January, February and March transitional water was sandwiched into a narrow zone between southern and northern water (Plate VII). As the boundaries of southern and northern waters moved apart during the early summer, the area occupied by transitional water increased until in August, September and October, it extended over the entire length of the British Isles. During August to November, transitional water penetrated northwards to Latitude 59° N. and at times apparently extended beyond the area sampled. A similar, but temporary extension occurred in May; by June, the boundary had reformed and it remained into July.

Periodically northern water intruded southeastwards towards Rockall Tablemount. In general the intrusions appeared to be weak. However, a strong intrusion occurred in May which, by June may have penetrated to coastal waters north of Eire and divided the transitional water into two. The broad zone of mixed northern and transitional waters in October, suggests another strong inflow may have preceded the sampling.

The distribution during 1957 of northern, southern and transitional water bodies was characterised by a consistent geographic relationship. Within the limits of the relationship there were variations. The most pronounced were seasonal and involved shifts in the location and extent of the areas covered by the water bodies, especially southern and transitional waters.

Northern and southern waters with additional properties

The T-S diagrams have indicated that waters of additional properties may be associated with northern and southern waters. The approximate geographic areas they occupy have been differentiated and the "fronts" (positions of steepened temperature gradients) between them and the more "usual" oceanic waters have been inserted (Plates VII to IX and Fig. 9).

The cool, low-salinity water associated with northern water was located towards the northwest limits of the sampled area. Plates VIII and IX illustrate irregular shifts in the position of the "front" between these waters. In July it was absent whereas it was present during May, June, August and September; it appeared to run obliquely towards, and then eastward along, the south side of Iceland in May and November, but this extension was not detected at other times. The charts also indicate that the "water of additional properties" would be represented in the T-S diagrams only when sampling extended far enough into the Atlantic on the more northerly routes. From January to April the routes were appreciably shorter and this water was not observed.

The warm water of high salinity associated with southern water, was located in the south (Plates VII to IX). Sampling there was erratic from January to May (there were no samples in June), and this water was not detected; either it was restricted to a small area and was not sampled, or was not present. In July, sampling was adequate and the warm, saline water was found over a broad area, northwards to between 46° and 47° N latitude. During August, September and October it maintained the northward position, encroaching on the area occupied by the southern water. In November the warm, saline water was just located, apparently having been replaced by very-high-salinity water; by December it was observed only in the extreme south of the area, in one series of samples.

It seems possible that, beginning in June or July, the warm, high-salinity water moved northwards, remained until the late summer and then retreated southwards during November and December. This advance and retreat may have been associated with summer conditions, unlike the counterpart in the north. These waters with the additional properties were geographically consistent which suggests they are more than a passing feature of the surface water in the area surveyed. The present study can offer no explanation for their presence.

High- and low-salinity pockets

In Plates VII to IX, the locations of the pockets of high- and low-salinity waters are shown. They were often numerous. A few covered considerable areas such as the low-salinity water in July in the northwest and in September in the north, and the pockets of relatively high-salinity water in July, August and September in the south and west.

Whenever very-high-salinity water was present it was located in, or extended outward from the Bay of Biscay. From January to April, high-salinity pockets were only doubtfully assigned to very-high-salinity water. There was stronger

evidence for its presence in May, although its geographic expanse was uncertain (Plates III and VIII). By July it apparently covered a wide area; there may have been a small isolated patch in August; it was not detected in September and occurred at only a few stations in October. In November it extended northwards and appeared to have displaced the southern water over a considerable area; it had almost completely disappeared in December. Very-high-salinity water thus was frequently, though irregularly detected in the south where it sometimes covered broad areas.

English Channel and North Sea

In the North Sea the general locations of water of 35.0‰ and above are shown (Plates VII to IX). From January to June and possibly in August, the Atlantic inflow, in the northern North Sea, lay remote from the coasts of Britain and Norway–Denmark, except for a second tongue extending towards the Skagerrak in February and March. In September, October, possibly in November, and in December, it shifted and then lay along the east coast of Scotland.

An origin (Smed, 1947; Fraser, 1952) for the Atlantic inflow could not be determined with finality. In July, four samples from the northwestern North Sea formed a separate group in Northern water in the T-S diagram (Plate IV). These observations can be interpreted as having been made from northern water (Plate VIII) in which case the inflow would have originated in that water.

The working T-S diagrams indicated that northern water may have again contributed to the inflow in February, March, April and June; but transitional water appeared to contribute in May, part of October, and in November. If these indications are correct, the oceanic influence in the northern North Sea in 1957 would have originated in waters with different properties. The strongest inflow occurred probably in late winter months, with some resurgence in June, in which case the chief influence would have been from northern water.

During several months water above 35.0‰ penetrated into the southern North Sea from the English Channel. Data are sufficient only to indicate that at times this water was most evident.

The T-S diagrams showed that waters from the northern coast of Scotland and the northwestern North Sea were often similar in properties. In Plates VII to IX the samples from these waters are seen to form a zone extending round the northern and down the eastern coasts of Scotland. Jacobsen and Jensen (1926) believed coastal water moved into the North Sea from the northern Scottish coast south of the Orkney Islands, and presumably the continuity of properties in the present study may be similarly interpreted.

Very-low-salinity water originating in the Baltic Sea was present in the Skagerrak during January, February and March. It was observed in the eastern North Sea in April; from May to September it covered a moderately large, variable area, which became reduced in size during October, November and December.

From the T-S diagrams it can be demonstrated that the properties of the water in the Western Channel and over the neighbouring shelf were similar at times. Hydrographic continuity between the two areas is indicated in Plates

VII to IX by means of a more or less complete tongue extending from the Western Channel in a northwest direction. Since it was present in 7 or 8 months, the situation it represents would seem to be a fairly sustained one. It does not appear to have been present in January, April and July.

There is a measure of identity between the properties of transitional and Western Channel waters in the T-S diagram for January (Plate I) and this has been interpreted (Plate VII) as indicating that transitional water was present in the area of the Western Channel. In February and March this water remained as small pockets, located further to seawards. There is only tenuous evidence that the transitional water reached the Western Channel by way of southward tongues in those months. In May, southwest of Eire, a narrow tongue extended briefly towards the south, and in Plate VIII it is suggested that mixed transitional and coastal water continued southward from this tongue. In July, a relatively large, tongue-like intrusion of transitional water may have moved southwards which, during August and September retreated northwards leaving pockets of transitional water and a mixture of transitional and southern waters behind. A broad southward intrusion of transitional water in October had disappeared by November. In December a tongue again appeared to extend south along the coast of Eire; this tongue could lead to conditions similar to those of the previous January.

There would seem little doubt that transitional water was directly influencing the water of the Western Channel in January (Plate VII); at other times the influence probably was less direct, through mixing with the inshore water. In either case the transitional water may have reached the Western Channel by way of the "tongues" which generally followed a curved course, somewhat east of south, towards the southern side of the entrance to the English Channel. Such a course lies to seaward of the proposed northwesterly course of Western Channel water.

It may be presumed these courses indicate a periodic southward movement of transitional water and a north–west movement of water from the Western Channel. Such movements were often concurrent. Taken together they are reminiscent of the anti-clockwise circulation for the area of the Celtic Sea (e.g. Lumby, 1925). The Western Channel water appears to have been influenced by transitional water during 7 or 8 months of 1957 (Plates VII to IX). If so, resemblances between the properties of Western Channel and transitional waters, instead of between Western Channel and southern waters, would be explained.

An influence of warm water in the Western Channel was observed in June and July (Plates III and IV). By August it had disappeared, but samples from further seaward (over the shelf) had temperatures similar to those previously recorded in the Western Channel. The distribution of southern water indicates it was intruding onto the shelf north of the Bay of Biscay in July and August, but that it had retreated by September (Plates VIII and IX). There is no evidence suggesting an origin for warm water in the Western Channel in June. If southern water intrusions were indeed the warm-water influence in the Western

Channel, it would appear to have been less direct than suggested by the charts since the increase of temperatures was not accompanied by an increase of salinities (Plates III and IV).

The surface water bodies defined from the T-S diagram clearly provide the basis for a complex distributional picture. There were two general features — the relatively large, permanent, southern, northern and transitional oceanic waters together with the coastal water bodies; and superimposed on oceanic waters were the waters of additional properties in the north and south and a variety of aperiodically occurring pockets of water of a wide range of salinities. The areas occupied by the oceanic water bodies fluctuated in size in a regular fashion, apparently in response to seasonal climatic effects. The Western Channel coastal water probably was influenced chiefly by transitional water extending southwards in narrow tongues; in turn these tongues appear to have been associated with a movement of water to the northwest, away from the area of the Western Channel. There are indications that the northern North Sea was influenced by both northern and transitional waters, and the northwestern North Sea by coastal water from the northern Scottish coasts.

GENERAL FEATURES OF THE SURFACE WATERS

Helland-Hansen and Nansen (1926) showed by means of density profiles that at 100 m, in about 25° W., the North Atlantic Drift divided and diverged. One branch moved northwards and then eastwards, the other (or part thereof) moved eastwards and southwards. Between the two branches was an area of weak, ill-defined currents and vortices. Tulloch and Tait (1959) show that in 1951, three streams approached Britain from the west, one north of about 60° N, another on a southeast course towards Rockall Tablemount, and the third in about 54° N. Sub-branches of the southern flow and the flow towards Rockall combined and contributed to a large, clockwise-circulating gyre west of Eire. A mixed water almost certainly resulted in the gyre.

Tulloch and Tait's circulation pattern is similar to, but is more detailed than that shown by Helland-Hansen and Nansen; both confirm the generalised picture obtained from the present study. The water comprising the northerly streams of these investigators is probably to be included in the northern water defined from the T-S diagram; the water of the southern stream is probably to be associated with southern water. The waters in the gyre are probably equivalent to the mixed transitional water.

Tulloch and Tait's flow towards the southern side of Rockall Tablemount possibly can be identified with the intrusions of northern water in 1957 shown in Plates VII to IX. The latter, however, were directed more usually towards the northern side of Rockall. Additionally, the distance penetrated by the intrusions varied from month to month. It appears that the location and strength of the intrusion may change over both short and long terms.

Tulloch and Tait also illustrate a south-going current along the northwest Irish coast which, from the interpretation in the present study, would probably consist of transitional water. This meets a north-going stream, along the

southern half or so of the coast, which was the shoreward side of a relatively small anti-clockwise eddy. The system may provide a situation whereby transitional water is able to intrude southward between the eddy and the Irish coast, especially in view of the mobility indicated by the short- and long-term fluctuations in the locations of the water bodies. An intrusion in these circumstances probably would remain a narrow tongue and be a temporary, although recurring feature, similar to those which were present on several occasions in 1957.

There was an unusual scatter of points in the T-S diagram for northern water in July (Plate IV), which, in the geographic presentation, indicated two features for the area south and west of Iceland (Plate VIII). There was no "front", as in June and August, between the "usual" northern water and water of lower salinities and temperatures; and there was a large body of dilute water (samples from which contributed to the scatter in the T-S diagram). Dietrich (1959) reported that surface-water observations from southwest of Iceland for July 1957 showed unexpected conditions, including low-salinity tongues (less than 35‰) extending from the northwest as far as the Reykjanes Ridge. The best defined of these coincides with the large patch of diluted water shown in the geographic chart (July, Plate VIII).

Where control is sufficient the location of the transition zone between oceanic and coastal waters (Fig. 2, 9) conforms fairly closely with the position of the edge of the continental shelf. It can be detected by salinity and probably by temperature changes. The salinities and temperatures at the last station in coastal water (shown by the T-S diagrams) and the first in oceanic water, approximately 10 miles further seawards, were subtracted on all lines of observations crossing the shelf; the differences for each month were averaged. The results are mean temperature and salinity differences across the "zone of immediate mixing" (Fig. 10a). The mean values for temperature indicate not only the gradient between the stations, but also reflect seasonal differential heating and cooling between coastal and oceanic waters. For example, in winter, spring and autumn, oceanic water was warmer than coastal waters; in summer, differences were variable, the oceanic water being slightly warmer than coastal water at times. Latitudinal differences also were apparent from a comparison of individual routes. Although a temperature gradient usually existed across the transition zone, it was not always in the same direction, or of the same magnitude. As a result, the use of temperature changes could cause confusion in locating the zone.

Mean salinities also varied on passing from coastal into oceanic water, but there was always a positive gradient (Fig. 10b). The least (mean) gradient was 0.16‰ in 10 miles (January); in April and June it reached 0.48‰. On individual routes the gradient varied between 0.1 and 0.97‰; values of about 0.5‰ were common. Thus, if the individual properties are being used, the salinity gradient may provide a more reliable guide than the temperature gradient for locating the zone between oceanic and coastal waters. However, there was little difficulty in reliably locating it with the aid of the T-S diagrams.

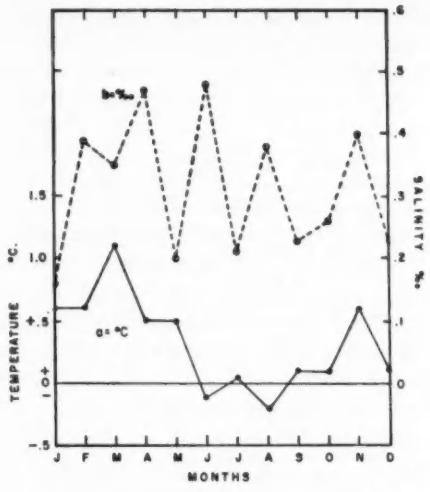

FIG. 10. The monthly means of temperature differences (line *a*) between the last station in coastal water and the first in oceanic water (as determined from the T-S diagrams), for all routes proceeding into the Atlantic from coastal waters. The monthly means of salinity differences (line *b*) determined in a similar manner to the temperatures.

DISCUSSION

The monthly T-S diagrams for 1957 have enabled a number of water bodies to be characterised for coastal and oceanic near-surface waters of northern Europe and the eastern North Atlantic. Relationships between the water bodies and effects of seasonal climatic fluctuations have been demonstrated. The diagrams also demonstrate the presence of various "extraneous influences" which add complexity to the surface waters. The distributional relationships between these several waters, month by month, have been demonstrated by presenting the data from the T-S diagrams in geographic charts.

The surface-water T-S diagram provides the means for identifying and defining the properties of "water bodies". It also enables those stations occurring in a particular water body to be identified; this ensures that the geographic location of the stations, and therefore the extent of the water body, can be determined. The validity of the T-S diagram for surface waters may be gauged against criteria such as whether it is sufficiently adaptable to be applied to all available data for the waters of one region under a variety of conditions and if so, does it supply a consistent, reasonable and readily interpreted picture. As has been demonstrated, the monthly diagrams for 1957 display a regular form or shape; they indicate the changes resulting on seasonal climatic fluctuations;

and the influences of other factors, of extraneous origin, are demonstrated. Moreover, when the data from the T-S diagrams are transferred to geographic charts, a picture is provided which appears to meet the general criteria. There seems little doubt that the technique contributes towards interpreting the characteristics of the surface waters.

SUMMARY

1. T-S diagrams of near-surface waters have been prepared for each month of 1957 for the oceanic area westward of Britain and southward of Iceland, and for the North Sea, English Channel and western approaches to the Channel.
2. The form of the T-S diagrams of oceanic waters is consistent from month to month. There are three parts which have been interpreted as three water bodies. These are cold, warm and transitional water bodies, the latter consisting of a mixture of the extremes; they are named northern, southern and transitional waters, respectively.
3. Coastal waters have been discussed as North Sea water, Western Channel water (between Land's End and Ushant) and water of the English Channel.
4. Other, spasmodically occurring pockets of water, were demonstrated in oceanic areas. These were of higher or lower salinity. Among the high-salinity pockets were ones in which salinities reached 36‰ and above. These were usually in or near the Bay of Biscay and are thought to have originated as surface water entering from outside the area sampled. This water is named very-high-salinity water.
5. All water bodies retained their identity throughout the temperature and salinity fluctuations in response to seasonal climatic changes. The *monthly* range of temperature of a water body may increase with summer conditions as in the North Sea, English Channel and transitional waters. Conversely, in northern and southern waters, and in the water of the Western Channel, there appeared to be "basic" monthly ranges of temperature and salinity of approximately 2 C°, and 0.2‰. Instances where increases of these monthly ranges occurred appear to have been due to other influences being imposed.
6. The limiting T-S properties of the water bodies have been contoured on to geographic charts in order to demonstrate the geographic relationships of the waters. Northern water was located north of the latitude (approximately) of northern Scotland. The northward extent of the spread of southern water fluctuated from about west of the English Channel in summer to westward of northern Ireland in winter. Transitional water occupied a comparatively narrow zone in winter, sandwiched between northern and southern waters, but a wide zone in summer when it extended further in both northward and southward directions.
7. There appears to be a fairly consistent oceanic influence in the area of the Western Channel which is regarded as frequently originating in transitional water; oceanic water entering the northern North Sea apparently may originate in either transitional or northern waters.

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REFERENCES

ANON. 1933. Atlas de température et salinité de l'eau de surface de la mer du Nord et de la Manche. *Service Hydrographique, Bur. Cons. perm. int. Explor. Mer, Copenhagen.*

1944. World Atlas of sea surface temperatures. *Hydro. Office, U.S. Navy*; HO. No. 225, 2nd edition.

BARY, B. M. 1959. Species of zooplankton as a means of identifying different surface waters and demonstrating their movements and mixing. *Pacific Sci.*, **13**(1): 14–54.

CARRUTHERS, J. N. 1927. Investigations upon the water movements in the English Channel, summer, 1924. *J. Mar. Biol. Assoc.*, **14**(3): 685–722.

COOPER, L. H. N. 1952. The physical and chemical oceanography of the waters bathing the continental slope of the Celtic Sea. *J. Mar. Biol. Assoc.*, **30**: 465–526.

1960. Some theorems and procedures in shallow-water oceanography applied to the Celtic Sea. *Ibid.*, **39**(2): 155–171.

1960a. The water flow into the English Channel from the southwest. *Ibid.*, **39**(2): 173–208.

CORBIN, P. G. 1947. The spawning of mackerel *Scomber scombrus* L., and Pilchard, *Clupea pilchardus* Walbaum, in the Celtic Sea in 1937–39. With suggestions on the zooplankton indicator species, *Sagitta* and *Muggiaea*. *J. Mar. Biol. Assoc.*, **27**: 65–132.

DIETRICH, G. 1959. Hydrographic details of the waters southwest of Iceland in July, 1957. *Cons. perm. int. Explor. Mer., Ann. Biol.*, **14**(1957): 22.

FRASER, J. H. 1950. Plankton investigations from Scottish research vessels. *Cons. perm. int. Explor. Mer, Ann. Biol.*, **6**(1949): 94.

1952. The Chaetognatha and other zooplankton of the Scottish area and their value as biological indicators of hydrographical conditions. *Mar. Res.*, 1952, No. 2, pp. 1–52. Scotland.

1955. The plankton of the waters approaching the British Isles in 1953. *Ibid.*, 1955, No. 1, pp. 1–12.

HARVEY, H. W. 1925. Hydrography of the English Channel. *Cons. perm. int. Explor. Mer, Rapp. Proc.-Verb.*, **37**: 58–89.

HELLAND-HANSEN, B., AND F. NANSEN. 1926. The Eastern North Atlantic. *Geofysiske Publikasjoner*, **4**(2): 1–75; Pl. 1–71.

JACOBSEN, J. P. 1934. Temperature and salinity at the surface of the North Sea and the English Channel. Description of methods used in preparing the atlas published in 1933. *Service Hydrographique, Bur. Cons. perm. int. Explor. Mer*, (*see also* Anon. 1933).

JACOBSEN, J. P., AND AAGE J. L. JENSEN. 1926. Examination of hydrographical measurements from the research vessels "Explorer" and "Dana" during the summer of 1924. *Cons. perm. int. Explor. Mer, Rapp. et Proc.-Verb.*, **34**: 31–84.

JOHN, DORA E., AND W. W. BROWN. 1958. Continuous plankton records: List of records, 1955–1957. *Bull. Mar. Ecol.*, **5**(4): 44–50; Pl. 9–14.

LUMBY, J. R. 1925. A note on the water movements in the English Channel and neighbouring seas, considered on the basis of salinity distribution. *J. Mar. Biol. Assoc.*, **13**(3): 670–672.

MILLER, A. R. 1950. A study of mixing processes over the edge of the continental shelf. *J. Mar. Res.* **9**(2): 145–160.

PICKFORD, GRACE E. 1946. *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. I. Natural history and distribution. *Dana Rept.*, **29**: 1–40.

1952. The Vampyromorpha of the Discovery Expeditions. *Discovery Rept.*, **26**: 197–210.

ROCHFORD, D. J. 1957. The identification and nomenclature of the surface water masses in the Tasman Sea (data to the end of 1954). *Australian J. Mar. Freshw. Res.*, **8**(4): 369–413.

RUSSELL, F. S. 1935. On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea. *J. Mar. Biol. Assoc.*, **20**(2): 309–332.

SMED, JENS. 1947. The inflow of Atlantic water into the North Sea through the Orkney-Shetland Channel. *Jour. Cons. perm. int. Explor. Mer*, **15**(1): 27–38.

1958. Charts of surface water temperatures and salinities, 1957. *Service Hydrographique, Cons. perm. int. Explor. Mer.*

SVERDRUP, H. J., M. W. JOHNSON AND R. H. FLEMING. 1942. The oceans, their physics, chemistry and general biology. Prentice-Hall Inc., New York, 1060 pp.

TAIT, J. B. 1937. The surface water drift in the northern and middle areas of the North Sea and in the Faroe-Shetland Channel. *Sci. Invest. — Fisheries*, Part II, Sect. 3, No. 1. Scotland.

TULLOCH, D. S., AND J. B. TAIT. 1959. Hydrography in the north-western approaches to the British Isles. *Mar. Res.*, 1959, No. 1, pp. 1–32. Scotland.

PLATES I-IX

PLATES I–VI

Temperature-Salinity diagrams of surface waters of the eastern North Atlantic and coastal areas of Britain, for each month of 1957.

LEGEND

Intercepts of Temperature and Salinity of Stations in:—

Oceanic water, i.e. from beyond the edge of the Continental Shelf.

Oceanic water occurring shorewards of the edge of the Continental Shelf.

Coastal water, on those routes passing over the shelf and into the Atlantic.

Coastal water, between Land's End and Ushant (Western Channel water).

Coastal water of the English Channel, between Dover-Calais and Land's End-Ushant.

Coastal water, North Sea.

Water Envelopes For:—

Oceanic water.

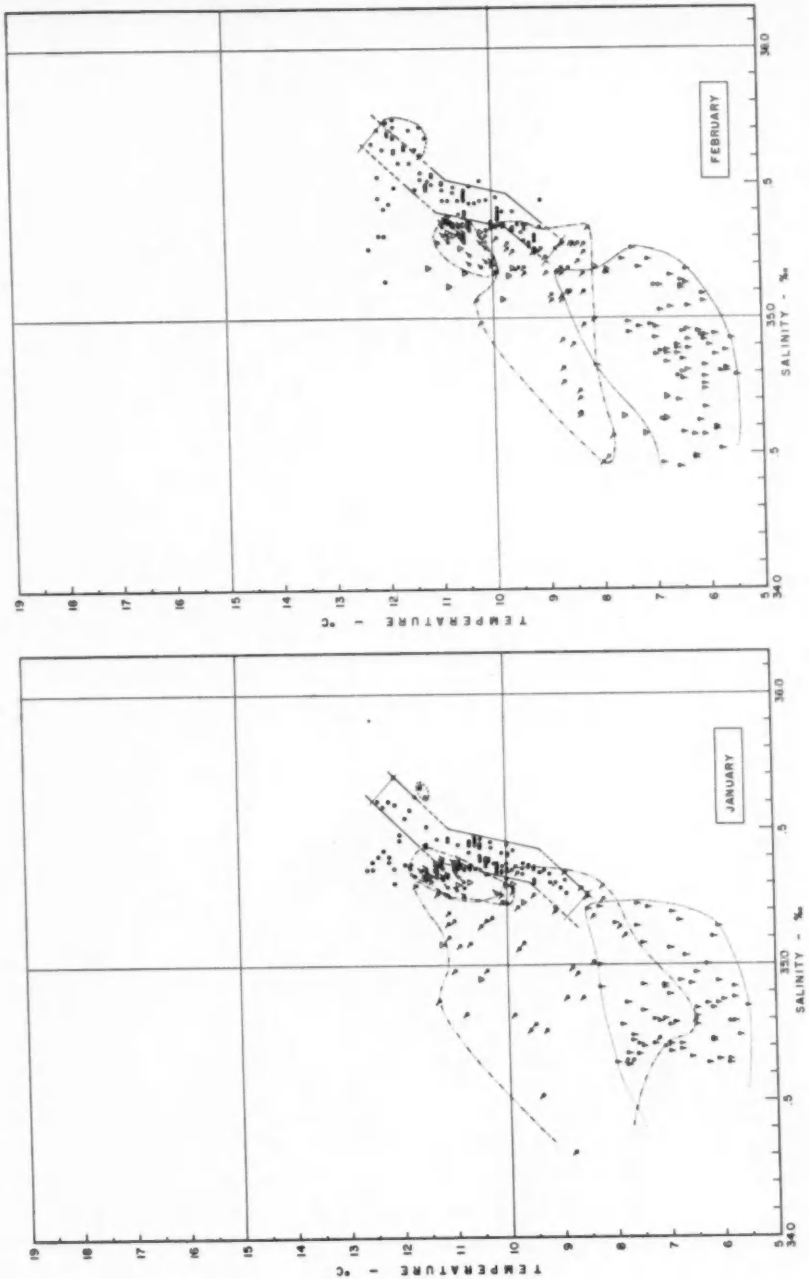
Oceanic water, interpretation doubtful.

Oceanic water, clouds of high-salinity water.

Coastal water, Land's End-Ushant.

Coastal water, English Channel.

Coastal water, North Sea.


FEBRUARY
JANUARY
TEMPERATURE - °C
SALINITY - ‰
19
18
17
16
15
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12
11
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9
8
7
6
5
340
350
360

Plate I.

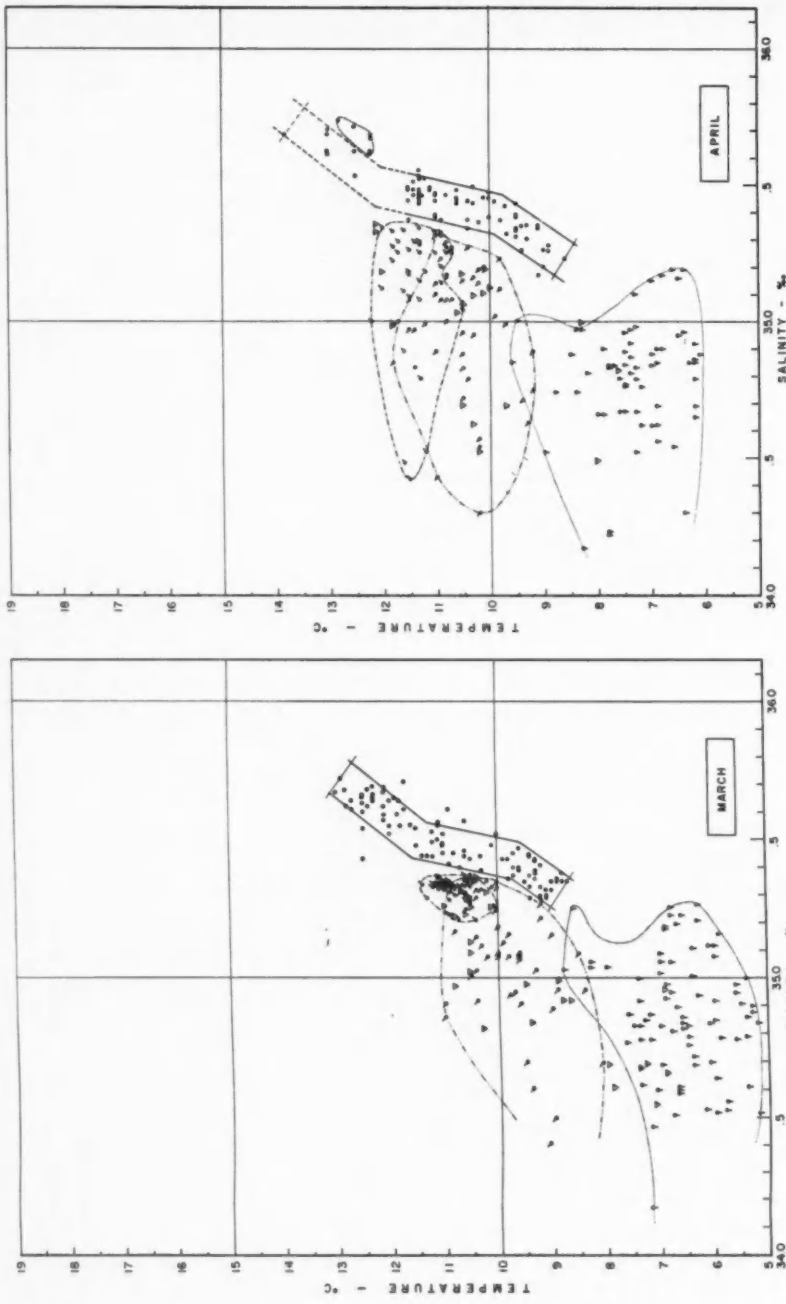
APRIL
MARCH
TEMPERATURE - °C
SALINITY - ‰
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Plate II.

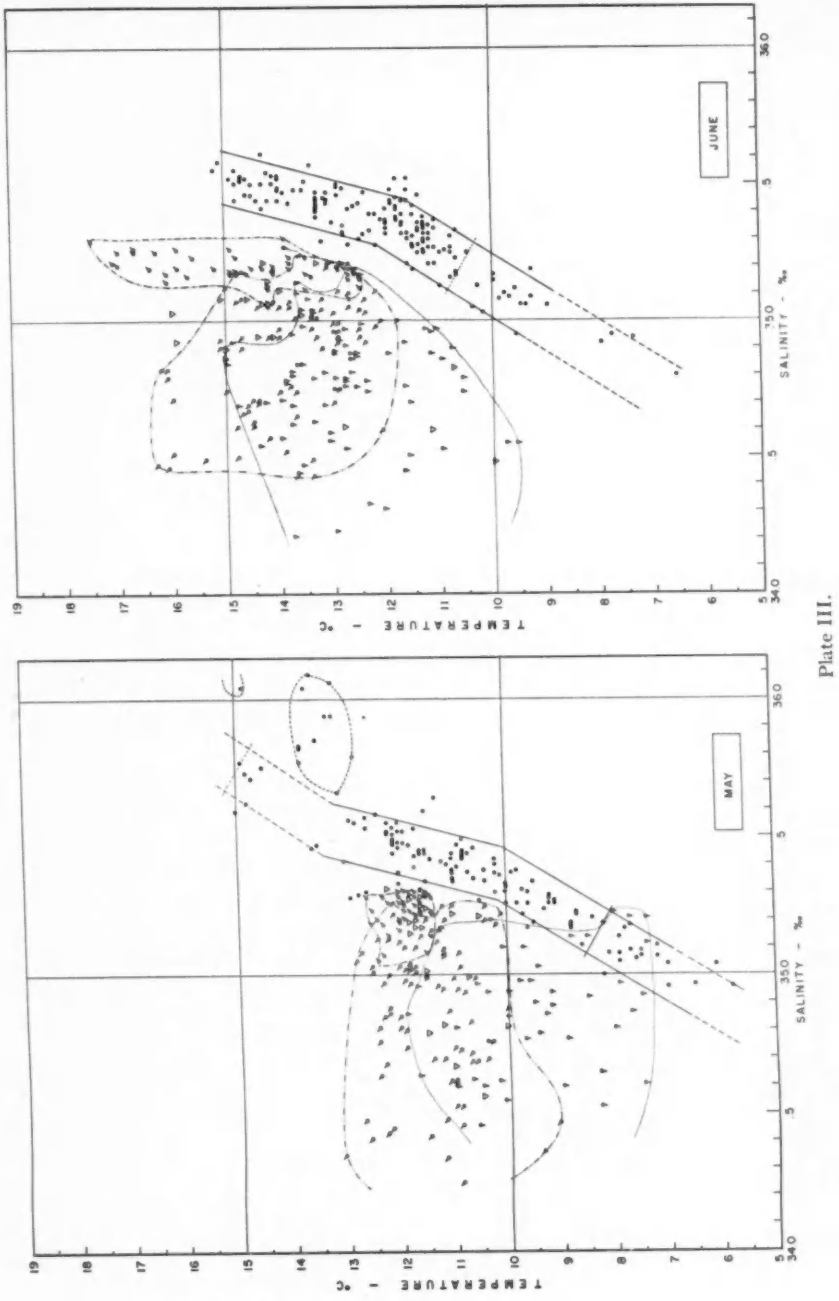

Plate III.

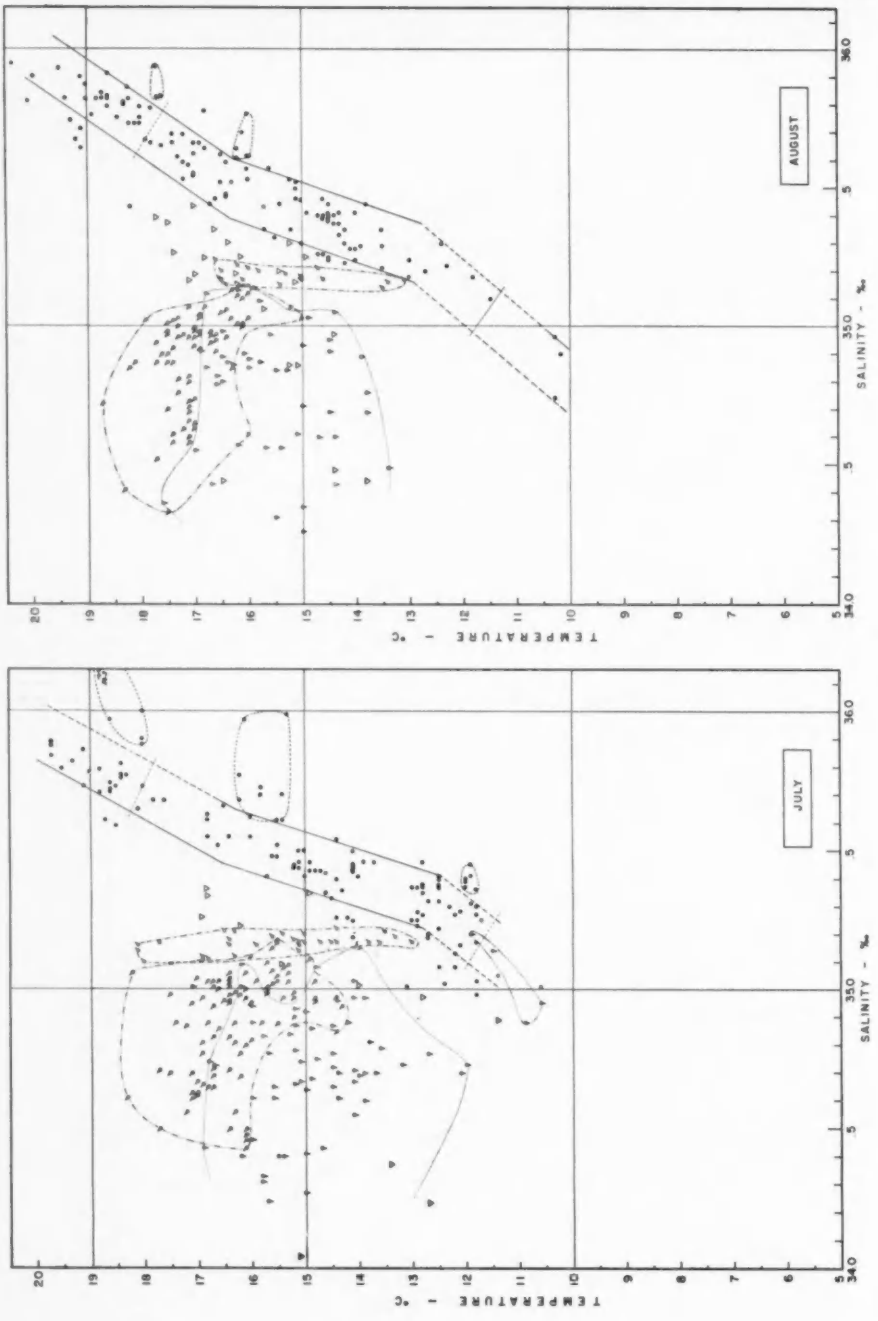
AUGUST
JULY
TEMPERATURE - °C
SALINITY - ‰
20
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Plate IV.

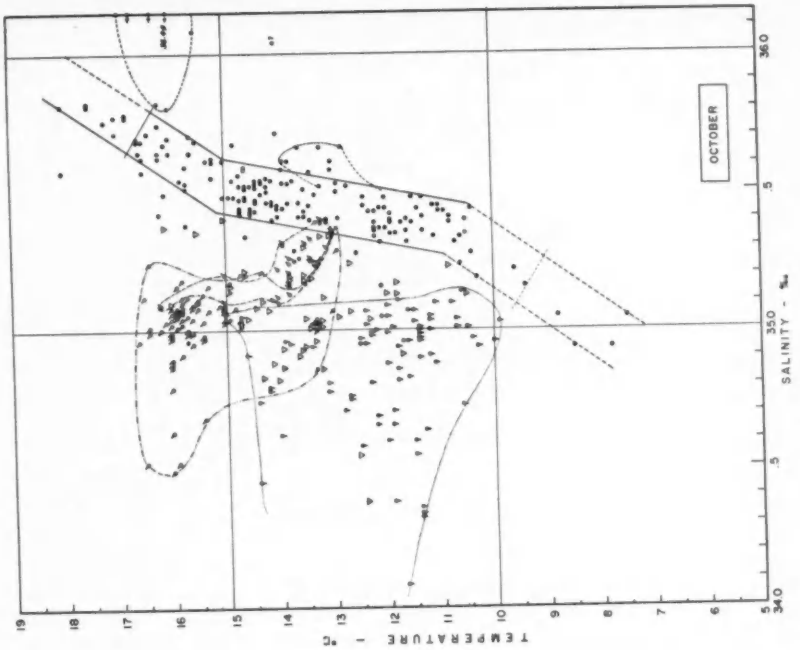

Plate IV.

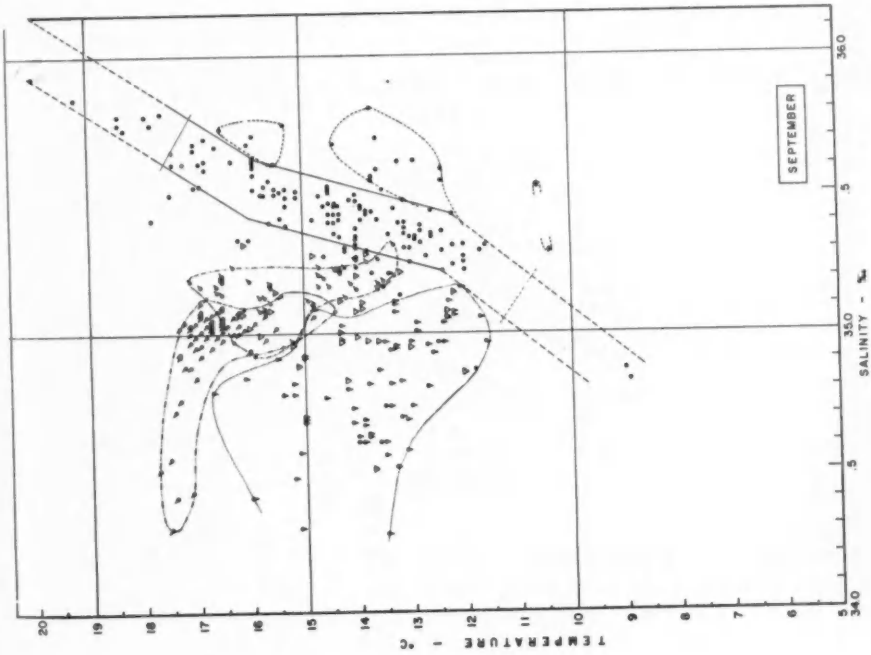

Plate V.

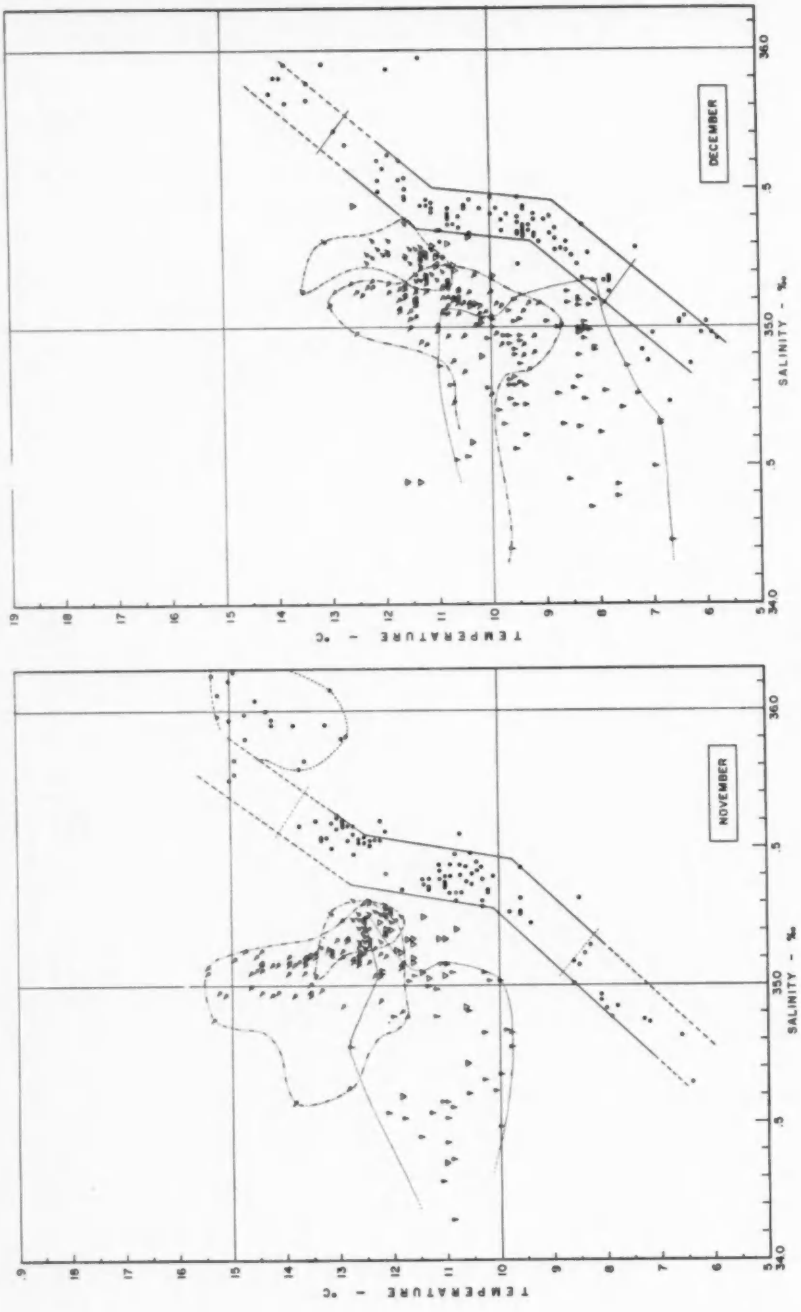
DECEMBER
NOVEMBER
SALINITY - ‰
TEMPERATURE - °C
360
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Plate VI.

PLATES VII TO IX

The distributions of water bodies, as characterised in the T-S diagrams, for each month of 1957.

LEGEND

All stations in oceanic water.

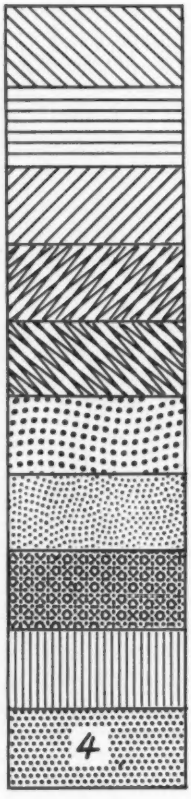
All stations in coastal water.

Water of 35‰ salinity and greater, North Sea.

Baltic outflow into North Sea, 34.1‰ and less.

Delimits water bodies.

Delimits water bodies, but conformation doubtful.



Northern oceanic water.

Transitional oceanic water.

Southern oceanic water.

Southern water of higher than usual temperatures and salinities.

Northern water of lower than usual temperatures and salinities.

Very-High-Salinity water.

Clouds of relatively high-salinity water.

Clouds of relatively low-salinity water.

Coastal waters.

The number of times during a month that observations were made along the neighbouring route (in coastal waters only).

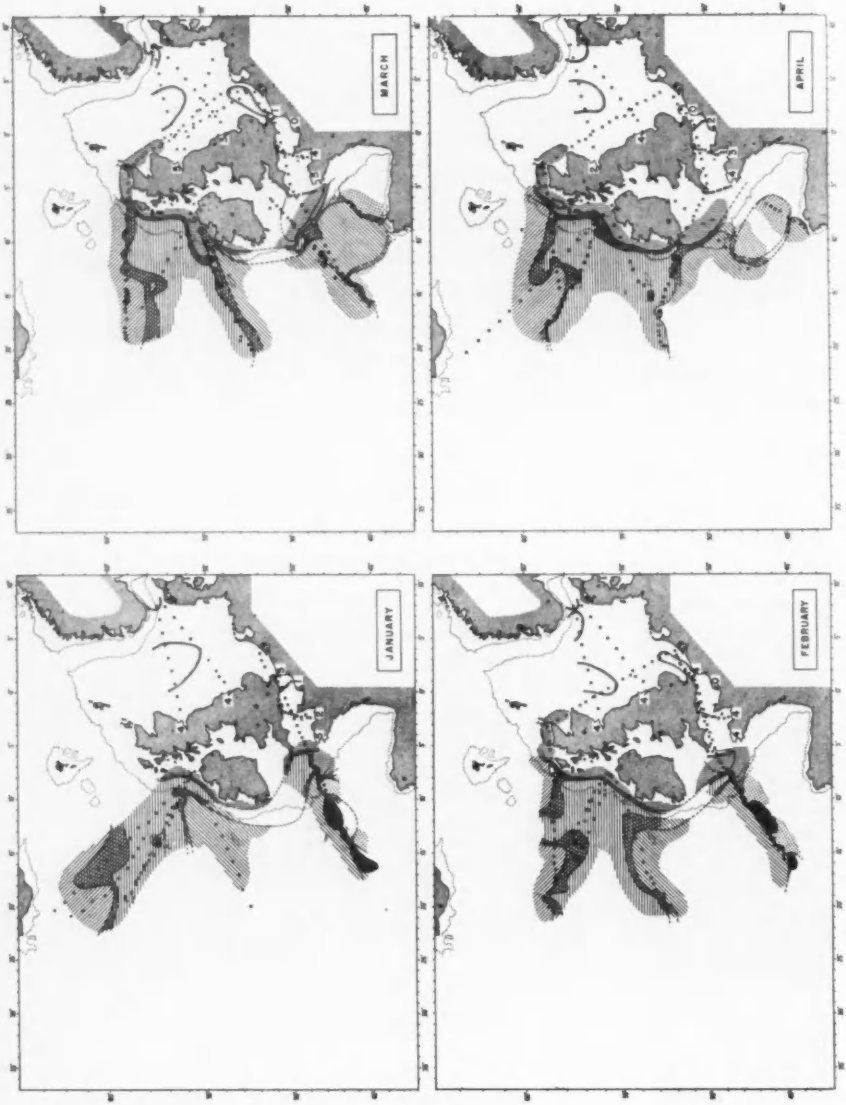


Plate VII.

Plate VIII.

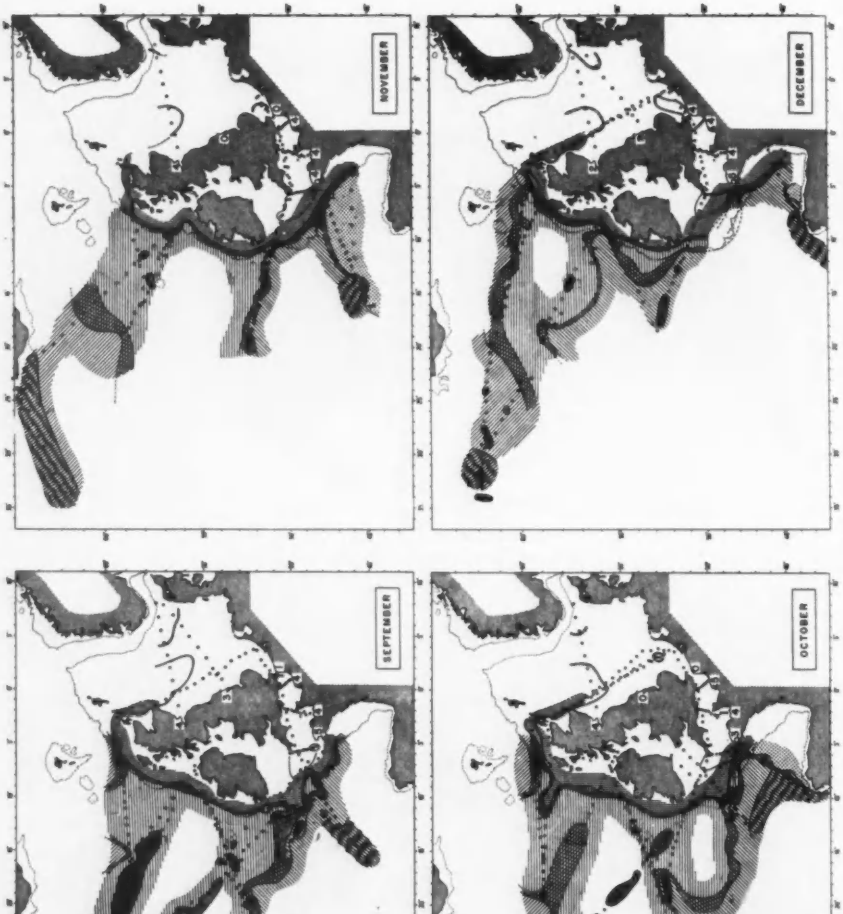


Plate IX.

The Uptake and Detoxification of C^{14}-labelled DDT in Atlantic Salmon, *Salmo salar*[1,2]

By F. H. Premdas and J. M. Anderson[3]

ABSTRACT

Atlantic salmon underyearlings were exposed to 1 ppm DDT-C^{14} and the amounts of DDT adsorbed to external surfaces and absorbed internally determined separately on the basis of the C^{14} activity. Fish killed by the exposure contained on the average 5.87 ppm DDT of which almost two-thirds represented absorbed DDT. After only 5 minutes exposure appreciable quantities of DDT were found throughout the body. At all times, up to and including the time of death, high concentrations of DDT were found in the gills, liver, spleen, heart, kidneys, gonads, and swim bladder. Much smaller concentrations occurred in the stomach, intestines, brain and spinal cord. The muscles, bone, and integument contained the least. It was concluded that DDT entered mainly through the gills from whence it was transported throughout the body via the circulatory system.

Bioassays showed that on the average almost two-thirds of the absorbed DDT was non-toxic, or at least relatively so, to mosquito larvae. The adsorbed DDT showed little, if any, loss of toxicity.

INTRODUCTION

Modern agricultural and silvicultural practices have frequently brought about contamination of fresh waters by DDT. This has resulted in widespread mortality of aquatic fauna among which the most sensitive forms are insects and fish (see Tarzwell, 1960, and Fettes, 1962). There is an appreciable range in sensitivity to DDT between species, but as a general rule a few hundredths of a part per million (ppm) is lethal to the majority of the species from both groups (Brown, 1951; West and Campbell, 1952).

In arthropods DDT enters chiefly through the cuticle. With regard to fish, the only work to date dealing critically with the uptake of DDT is that of Holden (1962). He concluded for brown trout, *Salmo trutta*, that the blood is the chief vehicle of transportation to the various organs where DDT deposition occurs more or less in proportion to the amount of contained lipid. Holden assumed that DDT must have entered mainly through the gills.

The metabolic fate of the absorbed DDT is also an important consideration. In insects it has been firmly established, particularly in houseflies, that DDT is degraded to non-toxic metabolites, notably DDE. DDE has been extracted from fish tissue (Cope, 1960) but direct evidence that fish can metabolize DDT appears to be lacking. In houseflies at least, it now seems certain that the DDT-

[1]Received for publication March 28, 1963.

[2]Contribution from the Department of Biology, University of New Brunswick, Fredericton, N.B. Based on a thesis submitted by the senior author in conformity with the requirements for the degree of Master of Science at the University of New Brunswick.

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J. Fish. Res. Bd. Canada, **20**(3), 1963.
Printed in Canada.

detoxifying enzyme, DDT-dehydrochlorinase, is responsible for the development of DDT-resistant strains (Brown, 1958, 1961). The question as to whether or not fish can degrade DDT may, therefore, be of far-reaching significance, a thought which is underlined by the recent report of the first instance of DDT-resistance appearing in fish (mosquito fish, *Gambusia affinis*, Vinson *et al.*, 1963).

The following is a report on the uptake, localization and detoxification of DDT in Atlantic salmon, *S. salar*.

GENERAL PROCEDURE

Ring-labelled, radioactive DDT (1,1,1-trichloro-2,2-bis-(4-chlorophenyl-4-C^{14}) ethane), specific activity 1.14 mc/mM, was used in all tests.

Radioactivity measurements were made with a Nuclear Chicago Model 183 Count-O-Matic Scaler with a 3053-Manual Sample Changer and a D-47 Gas Flow Counter.

Copper planchets, 3.1 cm in diameter, with their bases divided into five sections by four concentric rings, held the samples. Before use the planchets were washed and heated for twelve hours at 150°C. The copper-oxide surface so formed allowed for an easier and more uniform spread of material (Hogness *et al.*, 1948).

The Atlantic salmon used were underyearlings, obtained from the Department of Fisheries of Canada, Fish Culture Station, East Florenceville, N.B., and were kept at the University in 150-gallon fibre-glass tanks at 11 ±1°C. The fish were fed daily on ground beef liver. The water for the tanks was sand- and charcoal-filtered, and supplied from the city mains through plastic pipes.

The test animals were placed in a 2-litre beaker containing one litre of continually aerated water at 15 ±1°C. After about twenty minutes in the beaker the fish were exposed to 1 ppm DDT by adding 1 mg of DDT-C^{14} in 1 ml acetone. The average weight and length of the fish used were 5.2 gm and 70 mm, respectively.

After various times of exposure the fish were removed, one at a time, and rinsed thoroughly with two 5-ml portions of acetone to remove adsorbed DDT. DDT adhering to the surface of the gills was removed by holding the opercula open and allowing acetone to flow over the gills. The 10 ml of external wash for each fish was then transferred quantitatively to a copper planchet, care being taken to confine the solution to the four inner rings of the base. This had to be done slowly since each planchet could hold only about 2 ml of liquid. The transfer was carried out with the planchets on a slide warmer which hastened the complete evaporation of the acetone.

After washing off the external DDT, the fish were dissected and the various organs removed and weighed. Unless otherwise specified, the method of recovering the absorbed DDT was as follows. Each sample of fish tissue was placed in a porcelain mortar and ground for about ten minutes in 3–5 ml of acetone. The ground tissue–acetone mixture was then transferred to a 15-ml centrifuge tube. Two 3-ml acetone rinses of the mortar and the pestle were then added,

and the whole was centrifuged at 5000 rpm for five minutes. The supernatant was transferred to a copper planchet as described above for the external wash. The residue in the centrifuge tube was resuspended in 5 ml of acetone, centrifuged again and the supernatant added to the planchet. The resuspension process was repeated once more. A total of 19–21 ml of acetone, therefore, was used to extract the DDT from each sample.

No attempt was made to determine the amount of other extractable material besides DDT (e.g. lipid) which was also probably removed by the acetone.

Most, if not all, of the adsorbed DDT was removed from external surfaces by the one washing, because no, or at most only a slight suggestion of, radioactivity was detected in a second washing. This also indicated that no appreciable amount of DDT was washed out of the tissues of the fish. When the absorbed DDT was extracted from the various tissues, the first washing removed most, but not all, of the absorbed DDT. By the third washing, however, all of the DDT had been removed for neither further washings of the tissues nor the tissue residues themselves showed any remaining activity.

All radioassays were based on a linear relation between activity and DDT-C^{14} over the range used with a slope of 1502 ± 14 cpm per μg DDT-C^{14}.

RESULTS

In the first section of the results all activity is described as DDT although, as will be shown later, some activity may be associated with one or more degradation products. From the appearance of the planchets after the acetone had evaporated, it was evident that small amounts of non-volatile substances, probably fat, were being extracted in addition to the DDT and it was felt that this might seriously lower the radioassay count by self-absorption occurring within the sample. This was investigated by putting untreated fish through the normal extraction procedure and adding known amounts of DDT-C^{14} to the final acetone solutions. As expected, the radioassay calculations underestimated in every instance the amount of DDT known to be present. Generally, however, the error was less than 5%. It was decided, therefore, to let the radioassay calculations stand as uncorrected.

Recovery of DDT at Time of Death

Shown in Table I are the amounts of DDT recovered from 14 fish just after they died. Twelve of the fish had been placed in the exposure beaker in groups of three. Two others were exposed together. All fish died within 6 hours.

On the average, a total of 29.6 μg DDT-C^{14} per fish was recovered. Of this amount, a little less than two-thirds came from within the fish. The viscera (exclusive of the stomach and intestines) contained the highest concentration; gills ranked second, followed by the brain and spinal cord, and the stomach and intestines. The muscles, bones, and integument contained the lowest concentration.

It will be noted that while the gills, all the viscera, and the central nervous system together constitute only about 15% of the total body weight, they never-

TABLE I. Amount of DDT* recovered from extracts of macerated tissues and external wash of fourteen fish killed with 1 ppm radioactive DDT.

Preparation and tissue analyzed	Fish weight (gm)	DDT weight (μg)	DDT concentration (ppm)
External Wash			
Body and gills		11.41 ±4.10**	2.39 ±1.12
Extracts			
Gills	0.211 ±0.051	3.61 ±1.19	17.35 ±5.31
Stomach and intestines	0.275 ±0.073	2.77 ±1.29	10.07 ±3.89
Rest of viscera	0.161 ±0.042	3.75 ±1.0	24.77 ±8.35
Brain and spinal cord	0.081 ±0.017	0.92 ±0.23	12.71 ±4.46
Remains (muscle and skeleton)	4.23 ±0.93	7.14 ±3.38	1.77 ±0.98
Total absorbed	5.02 ±1.01	18.14 ±6.38	3.70 ±1.36

*The radioactive carbon recovered has been assumed to represent original DDT; that is, no attempt was made to determine the extent to which the radioactivity, particularly that of the extracts, might be associated with a degradation product of the original DDT.
**Mean ± standard deviation.

theless, contained a total amount of DDT one and one-half times greater than that in the rest of the fish.

TIME COURSE OF DDT UPTAKE

In order to study the rate of DDT adsorption and absorption, 2 lots of 6 fish were placed in exposure beakers, one lot per beaker, and treated with 1 ppm DDT in the usual manner. At various time intervals, individual fish were removed from each beaker. The external and internal DDT was recovered as previously described, except that here more organs were treated separately than was the case before.

The results are summarized in Table II which shows for each experimental fish and exposure time the amount of DDT recovered in ppm.

It is evident that after only 5 minutes exposure appreciable quantities of DDT were taken up by the fish. Thereafter absorption seemed to increase more rapidly than did adsorption until the time of death. This is more easily seen in Fig. 1 where the values in Table II have been averaged and plotted against time. After death there was an apparent reversal of DDT absorption. A massive change in permeability attending death, which allows DDT to escape from the body, is possible of course; it is also possible, however, that the decrease in DDT after death in our results is not significant, but merely represents the normal variation expected when only two fish are used for each time interval. It will be noted that the liver and spleen consistently contained the highest concentration of DDT; muscle and skeleton consistently contained the lowest. The general impression given is that extensive vascularization and DDT deposition go hand in hand. This is substantiated by the values in Table I, which, together with the general distribution of the DDT to all parts of the fish in only five minutes, indicates that gills are the main route of entry and the vascular system the chief means of transportation within the body.

TABLE II. Amount of DDT* recovered from external wash and extracts of macerated tissues of fish exposed to 1 ppm radioactive DDT for varying times.

	5 min		1 hr		2 hr		3 hr		4 hr (dead)		1 hr after death	
Weight of fish in grams	5.82**	5.89	4.07	3.46	5.18	4.85	4.98	4.47	5.09	3.93	4.80	4.15
External DDT (μg/g body weight)	1.24	1.11	4.18	2.18	4.18	2.44	4.29	2.71	3.99	4.44	6.78	3.28
Internal DDT (μg/g wet tissue (ppm))												
Gills	1.14	1.08	3.55	3.52	9.81	7.32	21.36	11.67	23.65	28.47	22.69	28.99
Stomach & intestine	0.11	0.36	2.24	0.16	3.01	3.54	4.51	3.60	17.38	15.89	5.98	8.81
Liver & spleen	1.56	1.71	31.03	6.48	26.99	28.00	61.52	40.94	72.53	56.03	47.13	44.51
Heart & kidneys	1.18	1.31	11.87	3.89	13.98	15.65	21.73	34.85	25.35	34.48	23.52	28.12
Gonads & swim bladder	1.69	1.00	7.50	1.58	15.03	6.51	21.06	32.37	23.40	35.33	23.82	53.57
Brain	0.34	0.30	2.59	1.12	5.43	3.92	9.61	12.78	15.49	24.76	18.43	9.48
Spinal cord	0.33	0.22	2.72	1.33	5.20	6.36	10.00	11.61	15.16	19.60	19.63	17.54
Rest of fish (muscles, bones & integument)	0.06	0.06	0.56	0.70	1.42	1.61	2.18	2.23	3.98	2.94	2.95	2.08
Total internal DDT	0.15	0.18	1.36	1.01	2.66	2.56	4.16	4.30	6.98	7.05	5.14	5.31

*The radioactive carbon recovered has been assumed to represent original DDT; that is, no attempt was made to determine the extent to which the radioactivity might be associated with a degradation product of the original DDT.

**The two lots of fish are separated by always recording the results for the same lot first.

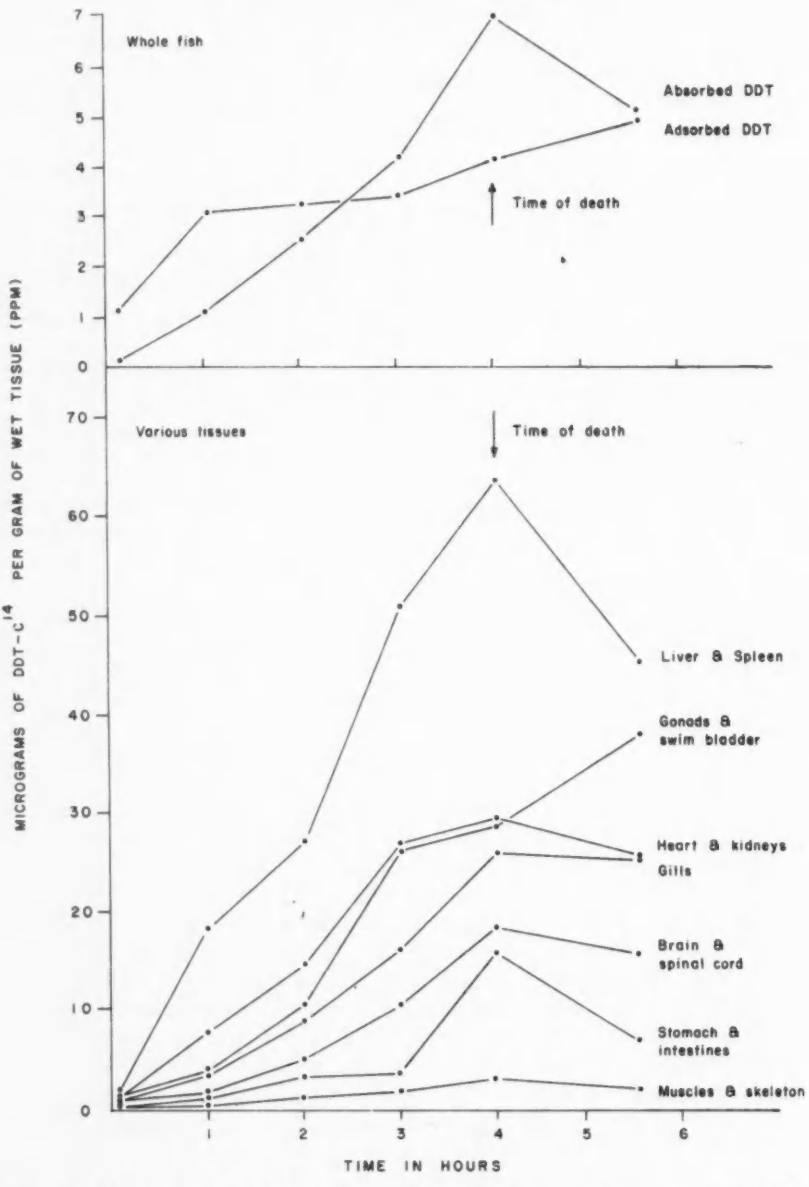

FIG. 1. The time course of DDT uptake. Each plotted point is the average for two fish. Concentration in ppm. The absorption and adsorption of DDT are shown for the whole fish (upper curves) and for various organs separately (lower curves).

DDT Detoxification

Detoxification of DDT by fish tissue was investigated by combining bioassay and radioassay techniques. The radiocarbon recovered from the fish was assayed for active DDT by determining the toxicity of the sample to mosquito larvae. The figures so obtained were then compared with the amount of DDT present, on the assumption that all the radioactivity was associated with the original DDT.

In more detail, the method was as follows. For the bioassay work, fourth instar *Aedes aegypti* larvae were used. They were reared after the method of Hartzell *et al.* (1958), except that tap water, instead of deionized water, was used throughout. The apparatus and method for detecting the presence of DDT is the same as that described by Hassett *et al.* (1960). In brief, the mosquito larvae, previously exposed to the DDT, or substance presumed to contain DDT, were placed in a plexiglas trough of triangular section with sides twelve inches long and three inches high, joined at their base to form an angle of 45°. The larvae in 250 ml of water, were confined by a gate to one end of the trough. A 60-watt bulb, situated behind the plexiglas at the end containing the larvae, was then turned on and the gate raised. Healthy, normal larvae moved quickly to the opposite end of the trough away from the light. DDT-treated larvae did so only with difficulty, if at all. Arbitrarily, any individual not able to reach the halfway mark in the trough in one minute after the light was turned on was considered to have been affected by the DDT. The degree to which the photomigration response was inhibited, i.e. the percentage of the sample not making it to the halfway point in one minute, was taken as a direct measure of the toxicity of the DDT. The method is surprisingly accurate. It is only necessary to ensure that each time an unknown quantity, or series of unknown quantities, of DDT is being assayed, a standardization run is made (using known amounts of DDT) with larvae from the *same* population as those used in the test run.

A group of 10 fish, 5 fish per exposure beaker, was killed with 1 ppm DDT-C^{14} in the usual manner. The fish from each beaker formed two separate series. Adsorbed DDT was removed in the usual way except that the 10 ml from each fish was not all transferred to one planchet. Instead, two 2-ml aliquots were plated separately and a radioassay made of these. Two more 2-ml aliquots were taken and each was added to a 400-ml beaker containing 200 ml of water. Twenty-five larvae, in 48 ml of water, were then added to make a final volume of 250 ml and the beakers then left undisturbed at 27 $\pm$1°C for 24 hours. At the end of this time the response of the larvae was observed. (The standardization runs, of course, employed known amounts of the same radioactive DDT that was used to kill the fish.)

Absorbed DDT was recovered as previously described except that here the entire fish was ground up at one time and only 12 ml of acetone was used in the process. Again, as with the external wash just referred to, duplicate radioassays and duplicate bioassays were made on 2-ml aliquots.

Just as there was concern that substances extracted along with the radiocarbon compounds might reduce the measured activity by physical masking,

so too there was some concern that a reduction in the toxic action of active DDT might result from a physical masking of the insecticide molecule by acetone-soluble substances. This possibility was investigated directly. Known amounts of DDT (from 1 to 16 μg) were added to 2-ml aliquots of acetone extracts obtained from untreated fish. Bioassays were conducted as if for unknown amounts of DDT. The response versus DDT concentration curve was superimposable upon the standard curve; that is, no detectable amount of masking had occurred. Of equal significance, these results also indicate that the fish extract *per se* was not toxic to the mosquito larvae. This was substantiated by other experiments designed specifically to investigate the point.

Results

The results of the two bioassay and radioassay series are shown in Table III. Considering first the external wash samples, it is evident that compared to the bioassay estimates, the radioassays tend consistently to give higher estimates of the amount of DDT present. On the average, however, the overestimation amounts to only 8%. Nonetheless, a paired t-test shows that the difference is significant ($P < .05$). Some transformation of the DDT to less toxic products must have occurred. It is difficult to imagine this occurring on the external surface of the fish. A more likely explanation for the difference is that small amounts of absorbed DDT from within the epidermis and perhaps also the gills, were removed together with the adsorbed DDT. This would imply that considerable detoxification of the internal DDT had taken place. This is confirmed by the results for the internal extracts where in every case but one the radioassay gives a larger estimate of the amount of DDT present by more than 50%. On the average, the overestimation amounts to 63%. Clearly, appreciable loss of toxicity of the DDT has occurred.

The most reasonable explanation for the loss of toxicity is that the absorbed DDT underwent degradation (chemical transformation) to one or more metabolites, such as DDE or DDA. Typically this is tacitly assumed in bioassay studies conducted similarly to ours (Lindquist *et al.*, 1951). Where they have been carried out, chemical analyses invariably have validated such an assumption. In insects, as already referred to, DDT is degraded to DDE. In mammals and birds DDA has been found frequently; DDE less so (Winteringham and Barnes, 1955). Reports on DDT metabolites in other vertebrates seem to be scarce. The DDE which Cope (1960) extracted from his fish could have come from ingested DDE-contaminated insects. It is important to note that our results do not give the precise percentage of the original DDT molecules that may have been metabolized. The lower limit is set by the percentages given in Table III. Theoretically, however, it is possible that all of the DDT was degraded, but to products with some residual lowered toxicity.

It is possible, although unlikely, that in our case no degradation of the absorbed DDT occurred. Once inside the fish the DDT, in amounts corresponding to the detoxification percentages given in Table III, may have been physically "surrounded" or otherwise have become combined with molecular components

TABLE III. Combined results of radioassays and bioassays on fish killed by 1 ppm DDT-C^{14}. Fourth instar larvae of *Aedes aegypti* were used in the bioassay. The standard curves for the bioassay series 1 and 2 were described by the linear regression equations $Y = 2.99 + 2.11\ X$ and $Y = 3.62 + 1.98\ X$ respectively, where Y is the percentage response of the larvae in probits and X is the log dose of DDT in μg.

Preparation		μg DDT in 2-ml aliquots on basis of radioassay(1)*	μg DDT in 2-ml aliquots on basis of bioassay (2)*	Percentage difference between (1) and (2)
External Wash				
Bioassay 1	#1	3.6	3.5	3
	2	5.5	4.6	16
	3	6.6	4.6	30
	4	3.7	3.5	5
	5**			
Bioassay 2	#1	5.6	5.4	4
	2	4.7	4.5	4
	3	5.0	5.0	0
	4	9.2	8.8	4
	5	8.2	7.8	5
		5.55±2.07	5.30±1.82	+ 7.9
Internal Extracts				
Bioassay 1	#1	3.7	1.7	54
	2	5.1	1.7	67
	3	4.2	1.6	62
	4	5.2	1.6	69
	5	4.3	1.6	63
Bioassay 2	#1	5.8	2.0	66
	2	4.9	1.3	73
	3	6.6	2.9	56
	4	6.8	3.6	47
	5	3.6	0.6	83
		5.02 ±1.12	1.86 ±0.83	+ 62.9

*Each value in this column represents the average of duplicate aliquot samples.
**The external wash of this fish was inadvertently spilled.

such that it was rendered non-toxic. In other words, the detoxification mechanism may have been physical rather than metabolic in nature. Under these circumstances a different extraction process might have released the DDT in the active form. This possibility is made remote, but not eliminated, by the fact that DDT added to fish extracts retained its full toxicity. Clearly the question can only be settled by chemical analyses.

DISCUSSION

The extremely rapid dispersal of the DDT to all parts of the body would indicate that the gills are the chief port of entry, and that the blood is the chief vehicle of transportation. It is nonetheless possible that some DDT enters via the integument since there is at the time of death almost as much DDT adsorbed to the outside as occurs internally and until just a short time before death there is actually more.

With regard to the total amount of DDT taken up by the fish, (i.e. adsorbed plus absorbed DDT) we obtained averages of 6.09 ppm (Table I) and 5.37 ppm (Table II, for those fish sampled after death) which when averaged together gives 5.87 ppm. Warner and Fenderson (1962) reported concentrations of DDT in ppm of 1.7 (minnows), 4.8 (sculpins), and 5.1 and 25.9 (brook trout) for fish killed by spray operations. Our values, then, are within the range found for fish killed in nature. It must not be inferred from this, however, that there exists for the fish as a whole a specific critical threshold of DDT concentration which, when reached, results inevitably in death. Holden (1962) found, for example, that while both his doses of 0.1 and 0.5 ppm DDT were lethal to brown trout, the fish exposed to the lower concentration had consistently lesser amounts of DDT in practically all of their tissues after death, both in terms of the total organ weight and the lipid fraction weight, than did the fish exposed to the higher concentration. Evidently the time courses for DDT uptake and DDT toxic action were not parallel. The possibility remains, of course, that there is a critical lethal threshold of DDT concentration in some target organ. Our results on the time course of DDT uptake do not indicate any one particularly likely candidate as a target organ. The problem is further complicated by the very real possibility that there may be significant variations between different organs in the rate of DDT detoxification. Thus the relatively small concentrations of DDT found in the central nervous system could be misleading if, for example, it turned out that this was all active DDT.

Of general interest is the observation that while DDT is noted for its extreme stability on the shelf and in aqueous suspension, it loses this stability very quickly inside living tissue. As our results show, on the average 63% of the absorbed DDT in the acetone extract is rendered non-toxic within at least four hours (the time of sampling) and very likely the time is considerably shorter than that. Further knowledge of the DDT detoxification mechanism, with special reference to its relative efficiency in the different fish organs would be particularly useful.

ACKNOWLEDGMENTS

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REFERENCES

BROWN, A. W. A. 1951. Insect control by chemicals. John Wiley & Sons Inc., N.Y.
1958. Insecticide resistance in arthropods. World Health Organ., Monograph Series No. 38. 240 pp.
1961. The challenge of insecticide resistance. *Bull. Entomol. Soc. Am.* **7**(1): 6–19.

COPE, O. B. 1960. The retention of DDT by trout and whitefish. Trans. 2nd Seminar on Biological Problems in Water Pollution. U.S. Dept. Health, Education, and Welfare.

FETTES, JAMES J. 1962. Forest aerial spraying — dosage concepts and avoidance of hazard to fish and wildlife. *Proc. Fifth World Forestry Congr.* (1960), **2**: 924–929.

HARTZELL, A., H. P. BURCHFIELD AND V. F. COTTY. 1958. Improvements in culturing larvae of *Aedes aegypti* (L) for use in insecticide bioassay. *Contrib. Boyce Thompson Inst.*, **19**: 321–325.

HASSETT, C. C., R. KIRK AND G. B. CRAIG. 1960. Apparatus for insecticide assay. *J. Econ. Entomol.*, **53**: p. 483.

HOGNESS, J. R., L. J. ROTH, E. LEIFER AND W. R. LANGHAM. 1948. The quantitative determination of C^{-14} activity in biological systems by direct plating. *J. Am. Chem. Soc.* **70**: p. 3840.

LINDQUIST, A. W., A. R. ROTH, W. W. YATES AND R. A. HOFFMAN. 1951. Use of radioactive tracers in studies of penetration and metabolism of DDT in houseflies. *J. Econ. Entomol.* **44**: 167–172.

TARZWELL, C. M. (Ed). 1960. Biological problems in water pollution. Compiled by C. M. Tarzwell from Trans. 2nd Seminar on Biological Problems in Water Pollution. U.S. Dept. Health, Education, and Welfare.

VINSON, S. B., C. E. BOYD AND D. E. FERGUSON. 1963. Resistance to DDT in the Mosquito Fish, *Gambusia affinia*. *Science*, **139**: 217–218.

WARNER, K., AND O. C. FENDERSON. 1962. Effects of DDT spraying for forest insects in Maine trout streams. *J. Wildlife Management*, **26**: 86–93.

WEST, T. F., AND G. A. CAMPBELL. 1952. DDT and newer persistent insecticides. Chemical Publishing Co. Inc. N.Y.

WINTERINGHAM, F. P. W., AND J. M. BARNES. 1955. Comparative response of insects and mammals to certain halogenated hydrocarbons used as insecticides. *Physiol. Rev.* **35**: 701–739.

NOTES

Application of the Paloheimo Linear Equation for Estimating Mortalities to a Seasonal Fishery

The popular form of the catch equation assumes that fishing and natural mortality occur uniformly throughout the year and from year to year. In the simplest form, which will be considered here, catchability is uniform from age to age also. Paloheimo (1961) discusses the use of the equation, with particular reference to the Beverton and Holt formula for estimating natural and fishing mortalities and develops a linear formula which provides a very easy solution.

The catch equation is

$$C = qf \int_{t_1}^{t_2} N(t)\, dt = \frac{qf\, N(t_1)}{qf + M} (1 - e^{-ZT}). \tag{1}$$

Here we shall treat the "instantaneous mortality rates" as rates and multiply them by the time over which they operate. Thus qf, M, and Z are the instantaneous fishing, natural and total mortality rates operating over the year and $T = t_2 - t_1$, where t_1 is the beginning of the year and t_2 the end. This point causes unnecessary confusion in the existing literature since the subscript "t" has been used to denote both a point of time (N_t) and an interval of time (Z_t) in the same equation. Subsequently, to keep the formulae simple, we shall designate years by 1 and 2 (rather than the conventional i and $i + 1$) and let it be understood that the age-groups have appropriately advanced from year to year.

No attention has been given, however, to the case where the fishing effort is concentrated into one season (say $\tau = 1$ month) but the natural mortality appears to be uniform throughout the year.

The catch equation for this case is

$$C = qf \int_{t_1}^{t_1 + \tau} N(t)\, dt = \frac{qf\, N(t_1)}{qf + M} (1 - e^{-(qf + M)\tau}) \tag{2}$$

and the population left at the end of the fishing season is

$$N(t_1 + \tau) = N(t_1)\, e^{-(qf + M)\tau}. \tag{3}$$

During the next eleven months this population is reduced by natural mortality alone, so that

$$N(t_2) = N(t_1)\, e^{-qf\tau - M\tau}\, e^{-M(T - \tau)}.$$

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Therefore,

$$N(t_2) = N(t_1)\, e^{-qf\tau - MT}. \tag{4}$$

Taking logarithms and rearranging, we get

$$qf\tau + MT = \log_e \frac{N(t_1)}{N(t_2)}. \tag{5}$$

Following the method of Beverton (1954) we can write, from our equations 2 and 5,

$$qf\tau + MT = \log_e \frac{C_1/f_1}{C_2/f_2} + \log_e \frac{Z_1}{1 - e^{-Z_1\tau}} \cdot \frac{1 - e^{-Z_2\tau}}{Z_2} \tag{6}$$

Using Paloheimo's equations (9) and (10) to approximate the Z terms on the right-hand side, the above equation becomes

$$qf\tau + MT = \log_e \frac{C_1/f_1}{C_2/f_2} + \frac{Z_1 - Z_2}{2}(\tau). \tag{7}$$

From Paloheimo's (15), and since T = 1 year,

$$\log_e \frac{C_1/f_1}{C_2/f_2} = q\frac{f_1 + f_2}{2}\tau + M. \tag{8}$$

This is identical to Paloheimo's equation except for the term "τ". Since τ is some given fraction of the year ($\frac{1}{12}$ in this case), then a seasonal fishery would give the same solution as a year-round fishery with the same total effort. For the seasonal fishery, the daily effort values are 12 times those for the year-round fishery but they are in operation for only $\frac{1}{12}$ (τ) of the year.

Thus the serious restriction, of year-round fishing, apparently inherent in the Beverton and Holt formula, is removed in Paloheimo's approximation. Provided all other conditions are met, catch-per-unit-effort data from seasonal fisheries may be used for the estimation of natural and fishing mortalities.

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REFERENCES

BEVERTON, R. J. H. 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. *U.S. Fishery Lab., Beaufort, N. Carolina, Misc. Contr.*, No. 2, 159 pp.

PALOHEIMO, J. E. 1961. Studies on estimation of mortalities. I. Comparison of a method described by Beverton and Holt and a new linear formula. *J. Fish. Res. Bd. Canada*, **18**(5): 645–662.

A Note on the Upper Lethal Temperature of Eggs of Two Species of *Triaenophorus*

It has been demonstrated by Lawler and Scott (1954) that the southern limit of distribution of species of the pseudophyllidean genus *Triaenophorus* is not generally as far south as that of the final host the northern pike, *Esox lucius* Linn., in North America. They postulate that spring or early summer temperatures corresponding to a 70°F July isotherm are critical for successful development. The similarity of the southern limit of distribution of *Triaenophorus* to an isothermal line was first pointed out by Dr W. A. Kennedy (cited by Miller, 1952).

Despite this field evidence which suggests that some upper limiting factor may be at work in controlling the southern distribution of the parasite, there is very little experimental evidence to back it up. Watson and Price (1960) found that exposures of infected cyclopids to temperatures of 30–35°C for short periods of time caused the death and rapid dissolution of procercoids of *T. crassus* and *T. nodulosus*. A series of preliminary experiments was undertaken in the summer of 1960 to give some information on the effect of high temperature on hatching and death of *Triaenophorus* eggs.

Eggs of *T. crassus* and *T. nodulosus* remain viable in a refrigerator for periods up to 3 weeks and will hatch in a few days without a great deal of mortality on being placed at room temperature.

Samples of eggs for the high temperature experiments were taken from successfully hatching stocks of *T. crassus* and *T. nodulosus* and placed in small vials containing well-oxygenated water. They were immersed in water baths at 29, 30 and 32°C. A control group was allowed to stand at room temperature which varied between 24° and 26°C during the experiment.

Subsamples were made at the beginning and after 6, 24, 30 and 48 hours to determine the number of live embryos in eggs, the number of dead eggs and the number of eggs hatched. The experiment was concluded after 48 hours (after 30 hours at 32°C) to avoid the possible effect of oxygen depletion.

Eggs were classed as dead if no recognizable motile embryo could be observed in them, and only those empty eggs with open opercula were counted as hatched.

Although the proportion of hatched eggs increased in some cultures and active coracidia were occasionally found in the subsamples, none of the samples was completely hatched at the termination of the experiment. Figures 1 and 2 show the changes in the proportion of hatched and dead eggs during the course of the experiment. This seems to indicate that at temperatures at or above 30°C the hatching of embryonated *Triaenophorus* eggs is retarded. In addition there is an increased rate of death of the embryos within the eggs.

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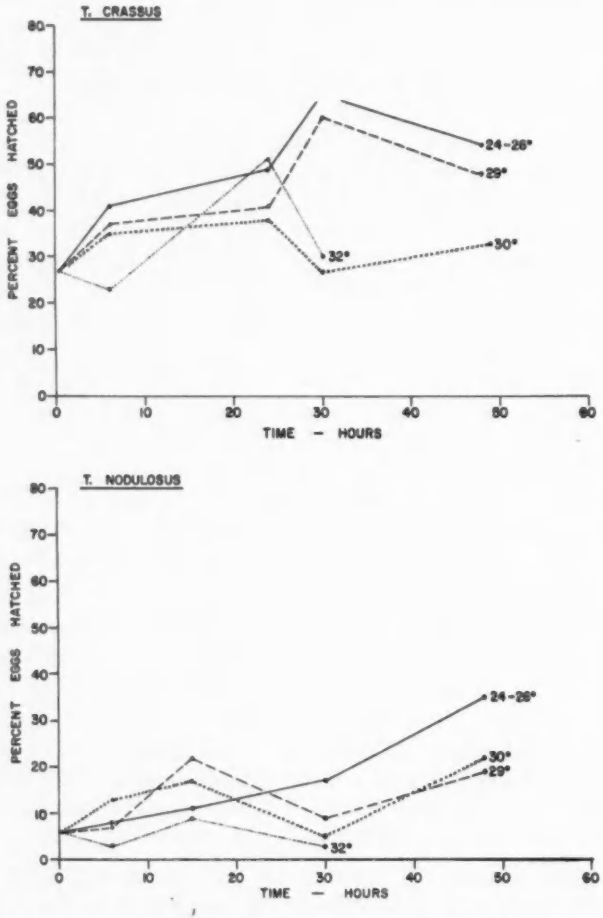

FIG. 1. Percentage of *Triaenophorus crassus* and *T. nodulosus* eggs hatched at temperatures between 24° and 32°C for several time-intervals.

A noticeable increase in the proportion of the eggs hatched occurred in the vials held at 24°C, but the hatching rate seemed to decline at the higher temperatures. Very little hatching was noted above 30°C. The proportion of dead eggs increased markedly in the cultures held at the elevated temperatures over the 48-hour period as compared to the control group at 24°C. This seems to indicate that at temperatures of the order of 30°C the hatching rate decreases and the death rate of embryonated *Triaenophorus* eggs increases.

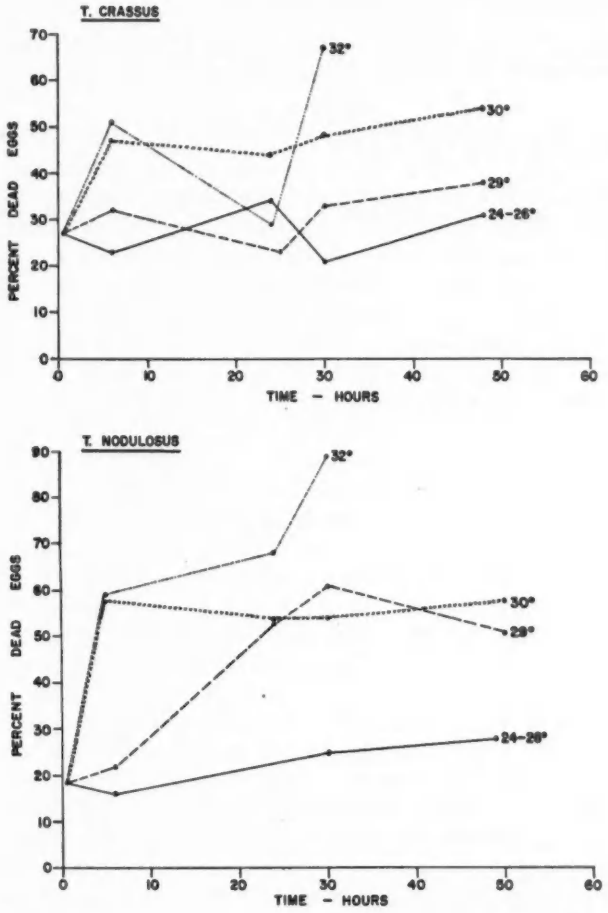

FIG. 2. Percentage of *Triaenophorus crassus* and *T. nodulosus* eggs dead at temperatures between 24° and 32°C for several time-intervals.

Further experimentation is required to relate these findings to conditions occurring in nature and to relate them to the distribution of the species within the range of its host.

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REFERENCES

LAWLER, G. H., AND W. B. SCOTT. 1954. Notes on the geographical distribution and the hosts of the cestode genus *Triaenophorus* in North America. *J. Fish Res. Bd. Canada*, **11**(6): 884–893.

MILLER, R. B. 1952. A review of the *Triaenophorus* problem in Canadian lakes. *Bull. Fish. Res. Bd. Canada*, No. 95, 42 pp.

WATSON, N. H. F., AND J. L. PRICE. 1960. Experimental infections of cyclopid copepods with *Triaenophorus crassus* Forel and *T. nodulosus* (Pallas). *Canadian J. Zool.*, **38**: 345–356.

On the Need for Measuring the Buffering Capacity of Fish Blood[1]

In a recent study of oxygen debt in fish (Hochachka, 1961), it became important to have some indication of blood buffering capacity. As a first approximation, the amount of hemoglobin was used to measure this capacity, since the role of the hemoglobin system in blood buffering is well known and fairly prominent. Moreover, the discovery that the respiratory function of hemoglobin might be of negligible significance in certain fishes (Anthony, 1961) seemed further to justify its choice as a measure of buffering. However, some preliminary tests show that several extrinsic and intrinsic factors affect the concentration of blood hemoglobin. The purpose of this note is to stress that for hemoglobin determinations to be of value it is important to define completely the conditions of the fish.

The experimental trout were of the stock described by Hochachka and Sinclair (1962) and Miller *et al.* (1959). The fish were of various but known ages, reared under hatchery conditions, and fed one of three types of food: Clarks or Encore pelleted rations or standard liver meals (see Hochachka and Sinclair, 1962, for further descriptions). Also, conditions were set up so that responses to physical training (i.e. maintenance in fast water currents) could be tested (Hochachka, 1961). Fish were netted directly from the holding tanks and killed immediately by decerebration. Blood for hemoglobin assay was drawn from the head wound with a small pipette. The entire process (netting fish and sampling) was completed within sixty seconds. Levels of hemoglobin were measured by the Haden-Hausser acid-hematin method. When applied to fish blood, this method, it is now recognized, is open to some question (Anthony, 1961). However, the data seem of sufficient interest to be presented, and hopefully might lead to a closer examination of the problem.

Measurements from several experimental groups are tabulated in Table I to show the effects of diet, age, and physical training on levels of blood hemoglobin. For the sake of comparison, samples obtained from wild trout indigenous to streams of the eastern slopes of the Rocky Mountains are included. The influence of physical training, diet, and age is evident in the Table. Younger trout had significantly higher concentrations of blood hemoglobin; as in the case of some mammals, this age-effect decreases with increasing age. Thus, the difference between ½-year-olds and 1-year-olds is greater than the difference between the 1- and 2-year-old trout. This age-effect is seen also in the samples taken from wild stock. The dietary influence is perhaps the least surprising. Differences between Clark-fed trout and the other two groups are significant but are not understood. Finally, the importance of changes in blood hemoglobin induced by training have been discussed previously (Hochachka, 1961) and need

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TABLE I. The concentration of hemoglobin in several groups of trout, expressed in grams per 100 ml of blood, with standard errors. Values marked with an asterisk are from Hochachka (1961).

Experimental group	Tested	Weight range	Age	Hemoglobin
	no.	*g*	*yr*	*g%*
Hatchery-reared fish				
Clarks trained	10	69–96	2.0	10.7 ± 0.20
Clarks trained	10	22–51	1.0	11.4 ± 0.25*
Clarks untrained	10	29–40	1.0	9.1 ± 0.20*
Clarks untrained	5	9–12	0.5	11.6 ± 0.51
Encore trained	10	22–47	1.0	9.9 ± 0.23
Liver trained	10	46–60	2.0	8.5 ± 0.24
Wild trout (from mountain stream)				
Salmo clarki	5	8–72	1–3	12.0 ± 0.33*
Salmo clarki	5	72–154	3–5	11.3 ± 0.18*
Salmo gairdneri	15	18–80	1–3	11.9 ± 0.20*

not be repeated here. The fairly high values obtained for the wild trout are also noted in that paper.

In addition to these factors, Black *et al.* (1962) have found that the concentration of blood hemoglobin is consistently altered during exercise, this process presumably being related to certain osmotic changes. And secondly, Prosser *et al.* (1957) have shown that acclimation to low oxygen tensions, like physical training, results in higher hemoglobin levels.

Thus, for a given determination to have any particular relevance, at least five factors—age, diet, physical training, exercise per se, and oxygen tension—must be defined or in some way be under control. It is concluded, therefore, that a hemoglobin index of buffering capacity is impractical for most purposes.

There are several reasons why measures on the buffering capacity of fish blood are requisite. For example, Black and his co-workers for some time now have been producing evidence of correlations between tissue acidity and death (see Black *et al.*, 1962); but the alternate and calculated approach of actually measuring buffering capacity has not been attempted, so the question remains: is it in fact within the capacity of fish blood to be able to buffer the large amount of lactic acid that is produced? That the answer is negative is supported indirectly by experiments in physically conditioning fish: since conditioning improved buffering capacity (Hochachka, 1961), it seems fair to assume that the buffer-gates of the unconditioned fish can indeed be flooded. More recently, Jonas *et al.* (1962) have made a more direct approach to this problem. Beyond certain pH limits, acidosis was shown to cause death. The limits and mechanisms of buffering systems available to the fish, however, need yet to be examined.

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REFERENCES

ANTHONY, E. H. 1961. Survival of goldfish in presence of carbon monoxide. *J. Exp. Biol.*, **38**: 109–125.

BLACK, E. C., ANNE ROBERTSON CONNOR, KWOK-CHEUNG LAM AND WING-GAY CHIU. 1962. Changes in glycogen, pyruvate and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. *J. Fish. Res. Bd. Canada*, **19**: 409–436.

HOCHACHKA, P. W. 1961. The effect of physical training on oxygen debt and glycogen reserves in trout. *Canadian J. Zool.*, **39**: 767–776.

HOCHACHKA, P. W., AND A. C. SINCLAIR. 1962. Glycogen stores in trout tissues before and after stream planting. *J. Fish. Res. Bd. Canada*, **19**: 127–136.

JONAS, R. E. E., HARCHARAN S. SEHDEV AND N. TOMLINSON. 1962. Blood pH and mortality in rainbow trout (*Salmo gairdneri*) and sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Canada*, **19**: 619–624.

MILLER, R. B., A. C. SINCLAIR AND P. W. HOCHACHKA. 1959. Diet, glycogen reserves and resistance to fatigue in hatchery rainbow trout. *J. Fish. Res. Bd. Canada*, **16**: 321–328.

PROSSER, C. L., L. M. BARR, R. D. PINC AND C. Y. LAUER. 1957. Acclimation of goldfish to concentrations of oxygen. *Physiol. Zool.*, **30**: 137–141.

A Note on *Gadus* (*Micromesistius*) *poutassou* (Risso) from Western Atlantic Waters

The blue whiting, *Gadus* (*Micromesistius*) *poutassou* (Risso), has been only recently reported for the western Atlantic, first by Bigelow and Schroeder (1955) who reported four specimens, one from Georges Bank and three from Browns Bank. In a recent cruise (Cruise 52) of the Fisheries Research Board of Canada research vessel *A. T. Cameron*, five specimens of *G. poutassou* were taken east of Sable Island, about Latitude 44° N., Longitude 59° W. This position is approximately 325 miles northeast of the Browns Bank specimens. The pyloric caeca counts, length and sex of these five specimens, plus similar data for Bigelow and Schroeder's specimens, are presented in Table I. Note that the smallest specimen, 201 mm in standard length, has the highest pyloric caeca count (15). The two larger females of the 1962 sample, numbers 4 and 5, were mature females with developing eggs in the ovary, and specimen number 1 was a mature male. There seems no reason to doubt that these represent a permanent population.

TABLE I. Length, pyloric caeca number and sex of *Gadus poutassou* from western Atlantic waters.

	1962 Captures					Bigelow & Schroeder (1955)			
Character	1	2	3	4	5	6	7	8	9
Standard length (*mm*)	201	230	238	284	302	322	347	357	388
Pyloric caeca	15	10	9	11	10	11	9	9	8
Sex	♂	♀	♀	♀	♀				

In a recent review Raitt (1962) summarized the available data on the numbers of pyloric caeca in the blue whiting and demonstrated a total range of 8–14 caeca from a study of 366 specimens from the eastern North Atlantic. Raitt's data, in the author's words "... suggest that the number of caecae tends to increase with size of fish." (In correspondence Raitt has indicated that statistical analyses have in fact shown that no clear-cut relationship can be demonstrated.)

The data presented in Table I are meagre and do not support the suggestion of positive correlation of pyloric caeca number with length of fish. It is of interest that the one count of 15 is higher than any recorded by Raitt for a large sample.

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Since the species appears to be a recent arrival in the western Atlantic observed differences from eastern Atlantic populations, in such characters as pyloric caeca number, would suggest environmental control. It is the author's hope that size, sex and pyloric caeca numbers of additional captures of this species in western Atlantic waters are reported.

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REFERENCES

BIGELOW, H. B., AND W. C. SCHROEDER. 1955. Occurrence off the middle and North Atlantic United States of the offshore hake *Merluccius albidus* (Mitchill) 1818, and of the blue whiting *Gadus* (*Micromesistius*) *poutassou* (Risso) 1826. *Bull. Mus. Comp. Zool. Harv.*, **113**: 205–26.

RAITT, D. F. S. 1962. A note on the pyloric caecae of *Gadus poutassou* Risso. *J. Cons. Explor. Mer.*, **27**: No. 1, pp. 49–51.

First Record of the Thornback Sculpin, *Paricelinus hopliticus*, Eigenmann and Eigenmann, in British Columbia Waters

Re-examination of a group of fishes collected by the junior author from Hecate Strait in 1952 revealed the presence of the thornback sculpin, *Paricelinus hopliticus* (Fig. 1). This is the first record of this species in British Columbia waters. The single specimen, a female, was caught in a shrimp trawl at a depth of 52 fathoms on rocky bottom 4 miles south of North Danger Rocks near Banks Island, Hecate Strait, on July 18, 1952. The fin ray counts and proportional body measurements of this specimen, 121 mm in standard length, were in complete agreement with those given for the species by Bolin (1944).

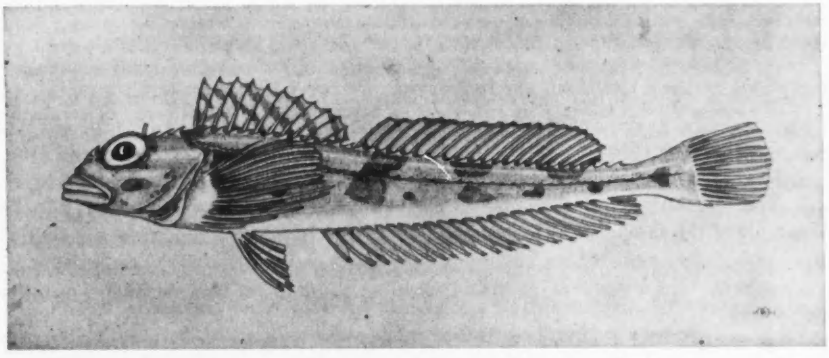

FIG. 1. Thornback sculpin, *Paricelinus hopliticus*, Eigenmann and Eigenmann, 1889.

This species was originally described (Eigenmann and Eigenmann, 1889) from Cortez Banks off San Diego, California, and has not been recorded previously north of the Oregon coast. Here it was recorded as *Alcidea thoburni* (Jordan and Evermann, pp. 1887–8, 1898). This new record represents a northern extension of range of about 700 miles.

The detailed description below follows the pattern adopted by Clemens and Wilby (1961):

Body elongate, moderately slender. Head small; mouth terminal, small; snout bluntly rounded, rather long; spines: nasal, well developed, sharply pointed, in line with profile of snout; 2 strong semirecumbent spines on fronto-parietal ridges, in line with single postocular spine; 2 small spines lateral to fronto-parietal ridge, in linear series with single, strong post-temporal; strong serrations and spines around orbits, occiput and suborbital stay; 1 or 2 on each of three posterior circumorbitals; 3 preopercular, simple; 1 on cleithrum behind end of opercular flap, strong; interorbital space narrow with deep V-shaped groove; gill membranes broadly united, free from isthmus for entire width. Anus immediately in front of anal fin, beneath 10th dorsal spine. Fins: dorsal (2), XII – 19; anal, 23; pectoral, 15; pelvic, I, 5. The last dorsal and anal fin element are split to the base and are counted as one ray. Spinous dorsal not emarginate; second dorsal contiguous to first dorsal, its origin about over 4th anal ray, markedly longer than first dorsal; anal nearly twice as long as second dorsal, origin about under next to last dorsal spine, similar in shape to that of second dorsal but emarginated; pectoral made up of two more or

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less distinct parts: the upper part of 9 rays bluntly rounded, with membranes not incised; the lower part with upper rays longer than rays immediately above, membranes deeply incised for half length of each ray; pelvis thoracic and reach past anus to second anal ray; caudal, truncate. Lateral line almost straight. Scales: body thickly beset with short, minute, slightly curved spinous scales; lateral line scales enlarged with bigger spines; a series of 34 or 35 much enlarged scales with hooked shaped spines extending along base of dorsal fins. Cirri: 1 on lower margin of suborbital; 1 on maxillary; 1 on cheek behind end of maxillary; 1 on posterior end suborbital stay; 1 at base of opercular flap; 1 on postorbital, large with fringed tip; 2 or 3 on margin of preoperculum.

The specimen in hand was preserved in formalin and naturally lacked colours with the exception of the dark melanin-like pigments on the first dorsal and body. Reference is made to Gilbert (1895) and Bolin (1944) for general colour notes. Colour: light olive green with 4 to 6 poorly defined brownish crossbands, 1 under spinous dorsal, 3 under second dorsal; sides below lateral line with 7 to 8 dusky purplish blotches; flecks yellow-brown along lateral line, a distinct series of small blue spots below it; lower surface whitish to light gray; first dorsal olive green with yellow-brown bars; second dorsal, caudal and upper half of pectoral transparent with brown rays; pelvics tipped with yellow.

Length to 7 inches.

Distinguished by a longitudinal series of scales along the base of the dorsal fin much enlarged with each scale bearing a prominent recurved spine, minute spinous scales covering body, three sharp preopercular spines directed backwards, sharp nasal spine, spines on occiput, along lower orbital margin and on suborbital stay, anal fin markedly longer than second dorsal, origin under first dorsal, pectorals with lower rays deeply exserted, a post-orbital cirrus with fringed tip.

This rare sculpin is known from rocky bottom between 48 and 100 fathoms. The common name "thornback sculpin" is most appropriate and is recommended by the American Fisheries Society (1960).

Range: Southern California to Hecate Strait.

The illustration of *Paracelinus hopliticus* (Fig. 1) was drawn by Mr D. Denbigh of the Biological Station, Nanaimo, British Columbia, from the British Columbia specimen. This specimen has been deposited in the collection of fishes at the University of British Columbia, and bears the catalogue number BC 62–541.

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REFERENCES

Anon. 1960. A list of common and scientific names of fishes from the United States and Canada. *American Fisheries Society, Special Publication* No. 2, 2nd ed., 102 pp.

Bolin, Rolf L. 1944. A review of the marine cottid fishes of California. *Stanford Ichthyological Bull.*, **3**(1): 1–135, Fig. 1–40.

Clemens, W. A., and G. V. Wilby. 1961. Fishes of the Pacific coast of Canada. *Bull. Fish. Res. Bd. Canada*, No. 68, 2nd ed., 443 pp.

Eigenmann, Carl H., and Rosa Smith Eigenmann. 1889. The fishes of Cortez Banks. *Cont. from the San Diego Biol. Lab. I. West American Scientist*, **6**: 123–131. San Diego, California.

Gilbert, Charles H. 1895. The ichthyological collections of the steamer Albatross during the years 1890 and 1891. *Rept. Commissioner, U.S. Comm. Fish and Fisheries*, Part 19, pp. 393–476, pls. 20–35.

Jordan, David Starr, and Barton Warren Evermann. 1898. The fishes of North and Middle America. *Bull. U.S. Nat. Mus.*, No. 47, Part 2, I–XXX, pp. 1241–2183.

First Records of *Tetronychoteuthis dussumieri* (d'Orbigny) (Cephalopoda; Onychoteuthidae) from the Northwest Atlantic

Five specimens of the onychoteuthid squid, *Tetronychoteuthis dussumieri* (d'Orbigny), were found in the stomachs of redfish, *Sebastes mentella* Travin, taken by C.G.S. *A.T. Cameron* on the eastern edge of the Grand Bank on September 15, 1961. The redfish were caught by otter trawl at Lat. 46°41′N, Long. 47°16′W at a depth of 280 fathoms (512 m), where the bottom temperature was 3.4°C.

The single specimen which was in relatively good condition (Fig. 1) was sent to Clarke by Rees for identification. The specimen was identified on the basis of the tentacle club, buccal connectives, shape, the papillae of the skin and the form of the mantle and funnel connectives which were all closely similar to *T. dussumieri*. The pen differed slightly from Pfeffer's (1912) description in its proportions and in having no ribs on the outer borders, but it was much closer to this species than to *Moroteuthis* or *Onychoteuthis*. The beaks also differed from those of *Moroteuthis* and *Onychoteuthis* in some respects. No nuchal folds were present but this may have been due to partial digestion by the redfish.

The other 4 specimens have been assigned to this species because they had the same characteristic skin papillae and colouration. Out of 41 redfish stomachs examined from this particular otter-trawl set, 17 contained the remains of squid, but only 5 were recognizable as *Tetronychoteuthis*. The preserved specimen has a dorsal mantle length of 10 cm, and the others were approximately the same size.

This is a very rare species being previously known in the Atlantic only from the stomachs of sperm whales, *Physeter catodon* L., taken near the Azores and Madeira (Clarke, 1956; Rees and Maul, 1956). The only other records are of two from the Indian Ocean, one from Mauritius and one from south of Australia (Pfeffer, 1912). Rees and Maul (1956) consider this species to be a member of the bathypelagic slope fauna, living close to the bottom in the 200–2000 m depth range.

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REFERENCES

CLARKE, R. H. 1956. Sperm whales of the Azores. *Discovery Rept.*, **28**: 237–298.

PFEFFER, G. 1912. Die Cephalopoden. Ergebn. Atlant. Plankton Exped. II, F. A., 815 pp., 48 plates.

REES, W. J., AND G. E. MAUL. 1956. The cephalopoda of Madeira. *Bull. British Mus. (Nat. Hist.)*, **3**(6): 259–281.

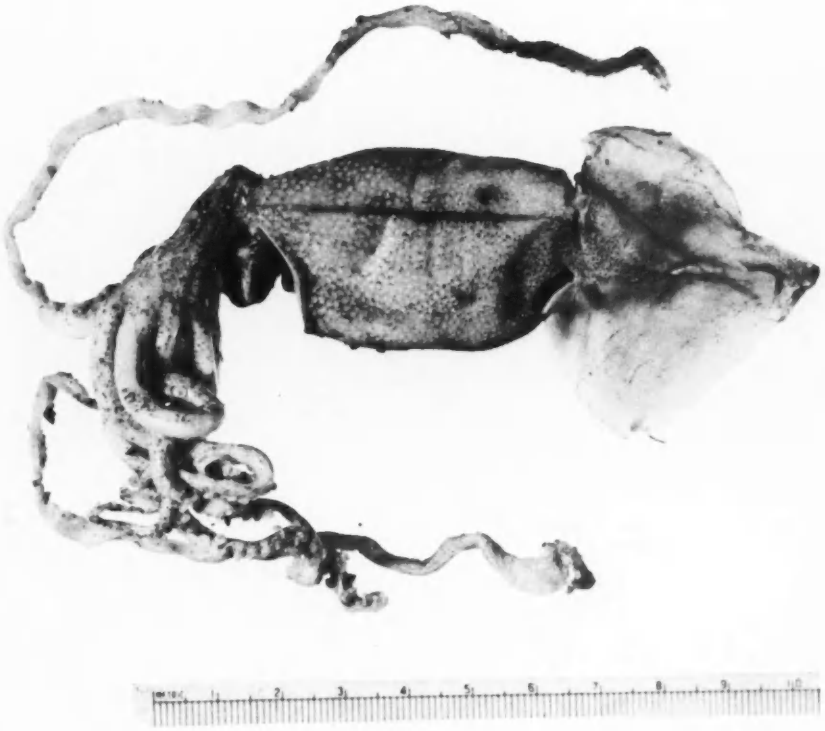

FIG. 1. *Tetronychoteuthis dussumieri* from redfish stomach, eastern edge of the Grand Bank, September 16, 1961.

Migrations of Haddock Between the Gulf of St. Lawrence and Offshore Nova Scotian Banks

Recaptures of haddock from a tagging in the southern Gulf of St. Lawrence have provided information about their seasonal distribution and movements in and out of the Gulf. There were 968 haddock tagged in the eastern end of Northumberland Strait (Fig. 1 and 2) in September and October 1956. They were captured by otter trawl and tagged with a modification of the Petersen disk tag, using a stainless steel wire through the back as described by McCracken (1956). All haddock tagged were of commercial size, with about 85% being between 45 and 55 cm fork length.

About 18% of the tagged haddock (171 fish) were subsequently recaptured. Recaptures continued at a relatively high level through 1959, about three years after tagging. The distribution of recaptured haddock in these three years is shown in Fig. 1 and 2.

From September to November, 1956, recaptures came mainly from the tagging region and have been omitted from Fig. 1 and 2. By December, recaptures were being made outside the Gulf of St. Lawrence from inshore grounds off the eastern coast of Cape Breton (Fig. 1). In February, March and April,

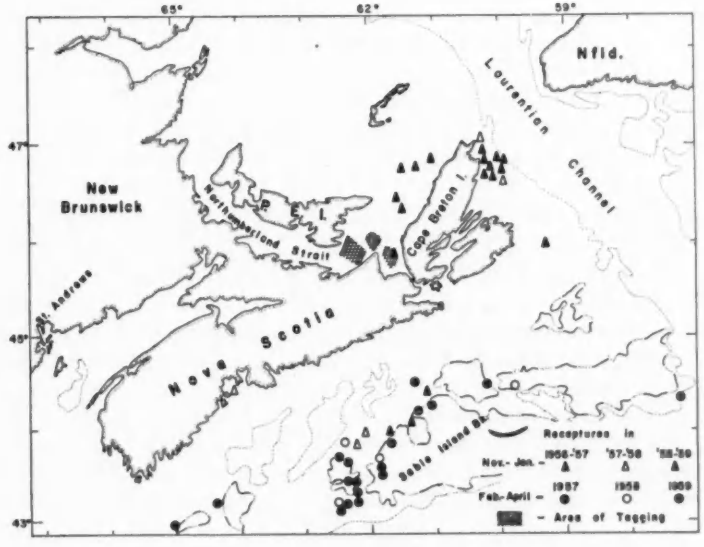

FIG. 1. Recaptures of haddock during the fall and winter of 1956 to 1959 from fish tagged in eastern Northumberland Strait in September–October, 1956.

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tagged fish were being retaken offshore, mainly from Sable Island and Emerald Banks off central Nova Scotia. A few fish were recaptured as far west as LaHave and Browns Banks, off western Nova Scotia.

In late spring and early summer (May–July) recaptures were again from inshore waters off the east and west coasts of Cape Breton (Fig. 2). Later in the season (August–October) recaptures were being made near the tagging region in eastern Northumberland Strait.

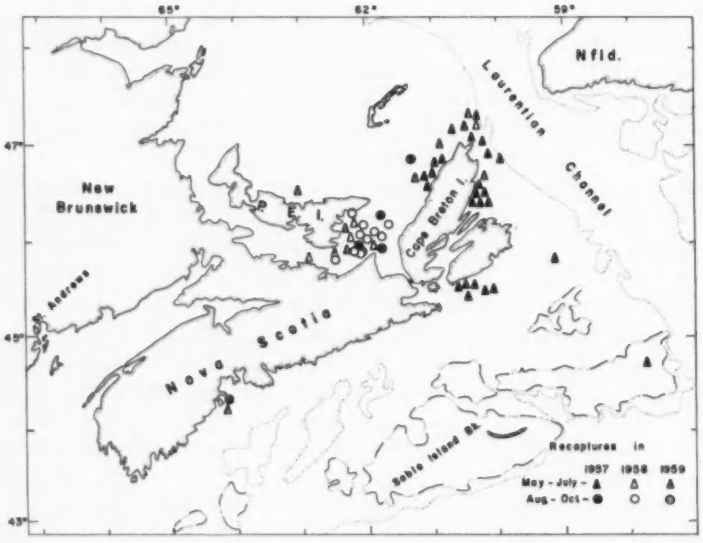

FIG. 2. Recaptures of haddock during the spring and summer of 1957 to 1959 from fish tagged in eastern Northumberland Strait in September–October, 1956.

Recaptures of tagged fish in 1958 and 1959 showed a seasonal recovery pattern similar to that for 1957—offshore in "winter", inshore off the east and west coasts of Cape Breton in spring and fall, and further into the Gulf of St. Lawrence in summer.

Haddock tag recaptures from eastern Nova Scotia and the Gulf of St. Lawrence reflect the seasonal nature of the inshore fishery there, as shown by the haddock landings for 1956–57 in the Table. Haddock landings by inshore boats and medium trawlers are negligible in winter from both regions. The large number of tags retaken off Cape Breton in spring and fall reflects the relatively large landings by small boats in all the eastern regions and the landings by medium otter trawlers in eastern Nova Scotia and the southern Gulf of St. Lawrence (Table I).

Tag recoveries from offshore banks in winter (February–April) came from the concentration of haddock off central Nova Scotia, which, in most years,

TABLE I. Landings of haddock by Canadian vessels from December 1956 to October 1957.

	Small boats	Otter trawlers	
		Medium	Large
	tons	*tons*	*tons*
Southern Gulf			
Dec.–Jan.	0	218	29
Feb.–Apr.	5	0	0
May–July	4	757	34
Aug.–Oct.	24	674	1
Eastern Nova Scotia			
Dec.–Jan.	190	168	223
Feb.–Apr.	34	80	1180
May–July	459	470	1758
Aug.–Oct.	155	115	806
Central Nova Scotia			
Dec.–Jan.	365	162	641
Feb.–Apr.	370	1254	6669
May–July	502	1316	3279
Aug.–Oct.	175	344	3021

supports the most important portion of the Canadian mainland haddock fishery. However, in 1957, haddock fishing continued at relatively high levels on offshore banks from May to October. The lack of tags from the offshore region in this period indicates that the haddock, which these tagged fish represent, had left the offshore region in summer.

The pattern of haddock tag recoveries is consistent with the hypothesis that the haddock which spend the summer in the southern Gulf are a migratory stock. These fish in passing off Cape Breton in spring and fall are the basis of the spring trap fishery there and the small otter-trawl fishery in the fall. In winter they form part of the stock fished on the offshore Sable Island and Emerald Banks, and intermingle with other haddock which concentrate in this region.

Mr C. J. Bayers carried out the tagging off eastern Prince Edward Island, ably assisted by Captain Butler and the crew of the M. V. *Harengus*. The co-operation of fishermen, fish processors and fishery officers in saving and returning tags has been most gratifying. The help of our technical, clerical and stenographic staff in recording and processing tag and reward information is gratefully acknowledged.

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REFERENCES

McCRACKEN, F. D. 1956. Cod and haddock tagging off Lockeport, N.S. *Fish. Res. Bd. Canada, Atlantic Prog. Rept.*, No. 64, pp. 10–15.

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Second edition of Bulletin No. 69. Fishes of the Pacific Coast of Canada. By W. A. Clemens and G. V. Wilby. (1961, 443 pp., $6.50 cloth-bound.)